II. *On the Morphology of the Cephalous Mollusca, as illustrated by the Anatomy of certain Heteropoda and Pteropoda collected during the Voyage of H.M.S. "Rattlesnake" in* 1846–50.

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"THE mere description of appearances even of the interior structure, still less of the exterior surface of an animal, without the deductions which they legitimately yield, is of comparatively small value to the philosophic naturalist; for of what value are facts until they have been made subservient to establishing general conclusions and laws of correlation, by which the judgment may be safely guided in regard to future glimpses at new phenomena in nature*?"

If I prefix this admirable exposition of the true aims of anatomical investigation to the present essay, it is that I may justify, by the highest authority, the course which I have taken in considering what of new facts it contains, as of subordinate importance to the reasonings which may be based upon those facts; in making its scope more morphological than zoological.

The morphology of the Cephalous Mollusca is a subject which has been greatly neglected. No SAVIGNY has determined the homologies of their different organs, and so furnished the only scientific basis for anatomical and zoological nomenclature.

It is not settled whether the back of a cuttle-fish answers to the dorsal or to the ventral surface of a Gasteropod. It is not decided whether the arms and funnel of the one have or have not their homologues in the other. The dorsal integument of a *Doris* and the cloak of a Whelk are both called "mantle," without any evidence to show that they are really homologous.

Nor do very much more definite notions seem to have prevailed with regard to the archetypal molluscous form, and the mode in which (if such an archetype exist) it becomes modified in the different secondary types. So far as our knowledge goes among other forms of animal life, we invariably find that, whatever the subsequent variations and aberrations, the primordial embryonic form has its parts arranged symmetrically about a given axis.

No one imagines the Pleuronectidæ belong to an asymmetrical type because they are asymmetrical in their adult shape, and yet there is no stronger evidence for the very common assertion that the typical form of the Mollusca is spiral or asymmetrical†.

This unsatisfactory state of our knowledge appears to me to result from two causes;

* OWEN, Anatomy of *Spirula*, Voyage of Samarang, Zoology, p. 12.

† See Von BAER, Nova Acta Acad. Nat. Cur. vol. xviii. p. 753.

—first, from the want of a clear and definite conception of the fundamental varieties of molluscous structure, and of the nature of the changes in the relations of parts which constitute those varieties; and secondly, from the want of a due regard to the facts presented by the development of the different families, which must stand in the relation of cause to the varieties of form.

Now in order to the former end (the obtaining of a definite conception of the varieties of molluscous form), I propose to set forth the structure of certain Heteropoda and Pteropoda; pelagic animals so transparent, that a perfect knowledge of the arrangement of their parts may be arrived at by simple inspection, without so much as interrupting a beat of their heart.

Afterwards, I shall inquire how far the known laws of development account for these forms, and thence of what archetypal form they may be supposed to be modifications.

PART I.

I. *Anatomy of Firoloïdes* (Plate II. fig. 1).

The species of *Firola* which I examined appears to be identical with the *Firoloïdes Desmarestii* of MM. Eydoux and Souleyet*.

The animal may be described as a transparent cylinder about an inch long, and so generally colourless as to be hardly distinguishable in the water, except by the incessant flapping of its flattened ventral appendage (*pp*).

The only parts which present any colour are the buccal mass, which is brownish; the eyes, almost black, and the mass of the liver, which is brownish green; further, the anus has a pinkish tint.

Attached by a narrow root or pedicle to the ventral surface of the cylindrical body is the broad cheese-cutter-shaped foot, or as I propose to call it, *propodium* (*pp*). Its posterior edge is quite sharp, and carries no sucker-like expansion. The anterior fifth, or thereabouts, of the animal is thinner than the rest of the body, and it narrows again towards its extremity, which is truncated, and forms a circular lip round the aperture of the mouth. Just behind the narrowed fifth, and towards the dorsal surface, we observe the eyes, and immediately below, and as if proceeding from them, are the tentacles, which are short and conical.

The posterior extremity also is abruptly truncated; its uppermost angle slightly projects, and viewed from above appears like a subspiral, richly ciliated band (*d*). Some little distance from this is the aperture of the anus (*a*).

From the two inferior angles, two tubular processes pass in the male (fig. 1). The right process ends in a globular body and is the penis (*p*), while the left (which I shall call the *metapodium*) is long and somewhat pointed (*mt*).

In the female there is only one process (the metapodium) (fig. 2, 3 *mt*) answering

* Figured by them in their beautiful plates illustrative of the Zoology of the Voyage of the Bonite.

to the left of the male, but a long cylindrical egg-tube frequently trails from the aperture of the oviduct (fig. 2).

Alimentary System.—This consists of,—1, the buccal mass; 2, the œsophagus and stomach; 3, the intestine and its termination, the rectum; 4, the liver; and 5, the salivary glands, which are very small and placed above the buccal mass, contrasting singularly with the very large salivary glands of *Atlanta.*

The œsophagus, stomach, and intestine form a straight tube running through the axis of the animal, and suspended by a ligament to the dorsal parietes (fig. 1); having reached the "nucleus," that is, the mass of the liver and ovary, the intestine bends up at a right angle, and so becomes the rectum, which terminates, as has been seen, upon the dorsal surface.

The Buccal Mass, or Tongue (fig. 1 *b*).—This is an oval brownish body, placed below the commencement of the œsophagus, and forming the floor of the cavity of the mouth. The following parts may be distinguished in this mass:—

1. Two ovoid compressed masses of thick-walled clear cells, which somewhat resemble cartilage. I shall call these the "lingual cartilages."

2. These give attachment to muscular fibres by their outer surface, and are enveloped in them. One portion of these fibres is inserted anteriorly into the parietes of the body, and acts therefore as a protractor. The rest are inserted into the edges of a thin plate, the "tongue-plate," which is closely applied to the whole of the upper and a part of the anterior lower surface of the cartilages, being as it were bent over their anterior extremities. The applied surfaces of the plate and of the cartilages are perfectly smooth, so that the former can play readily over the latter, like a rope upon its pulley. The upper surface of the tongue-plate carries in the middle a single row of tridentate teeth; outside these is a row of conical spines and broad flat-edged plates, and most externally there are one or more rows of recurved hooks, which, when the organ is at rest, lie over and nearly meet one another in the middle line.

When this organ is in action, it is commonly more or less protruded from the mouth by the protractor muscles; the large lateral spines of the tongue are divaricated (giving rise to that resemblance to the oral armature of *Sagitta* which has been remarked), so as to get all the teeth to bear; and then by the alternate action of the upper and lower sets of muscles inserted into the tongue-plate, a chain saw-like movement is communicated thereto, in consequence of which the teeth act as a rasp or saw upon any body with which they are brought in contact.

The buccal cartilages take no part in the movement of the tongue-plate, but simply act as its pulley.

The *Œsophagus* widens so gradually into the stomach, that no distinct line of demarcation can be drawn between the two, but the latter narrows suddenly into the intestine at a short distance in front of the "nucleus."

The *Liver* (*l*) is composed of several foliaceous masses containing many oil-globules; it opens by a wide duct into the angle of junction of the intestine and rectum.

The Circulatory System (figs. 1, 2, 3, 6).—This consists of a very perfect heart with an aorta and its branches, but there is no trace of any venous system.

The heart lies anterior to and parallel with the rectum ; its axis therefore is nearly at right angles with that of the body. It possesses two chambers, an auricle (*u*) and a ventricle (*v*). The auricle is large and somewhat elongated, extending above into the elevation which carries the subspiral ciliated band. Its wall is formed by branched and interlacing muscular fibres, which are attached partly to the parietes, partly to the walls of a contractile sac (*c*), to be mentioned presently.

The ventricle is almost globular, and has thicker walls, in which the separate muscular fibres are not distinguishable. The lips of the auriculo-ventricular aperture are prolonged on the ventricular side into two valvular folds. Below, the ventricle terminates in a wide aorta, which immediately gives off a large branch backwards to the hepatic and generative organs; then becoming much convoluted, it runs forwards along the intestine and stomach, passing between the latter and the pedal ganglia (fig. 6), and finally terminating, without much alteration in its diameter, in the buccal mass.

As it passes over the pedal ganglia it gives off a considerable branch, "the pedal artery," downwards to the foot; and this pedal artery, just before it enters the foot, gives off a long and delicate "metapodal" branch (*w'*), which passes backwards, parallel to the aorta, and finally terminates in the metapodium, figs. 2 and 3.

The mode of ending of the pedal artery is very remarkable, and physiologically speaking, almost unique (fig. 6). Having entered the foot, it ends suddenly, without narrowing, in a truncated open extremity (*y'*). In the living animal this open end possesses the power of contracting to a very great extent, so as almost to become closed; and its condition must necessarily exercise a very considerable influence upon the direction and rapidity of the animal's circulation.

*Firoloïdes** then affords the most complete ocular demonstration of the truth of M.-Milne Edwards's views with regard to the nature of the circulation in the Mollusca, that can possibly be desired. The perfect transparency of the creature allows the corpuscles of its blood to be seen floating in the visceral cavity between the intestine and the parietes, and drifting more or less rapidly backwards to the heart. Having reached the wall of the auricle, they make their way through its meshes as they best may, sometimes getting entangled therein, if the force of the heart has become feeble. From the auricle they may be followed to the ventricle, and from the ventricle into the aorta, whence they pass, some forwards, to the buccal mass, in which the aorta ends, and through whose tissues it pours them; some downwards, to pour out of the widely open end of the pedal artery, flooding the tissues of the propodium; and a small proportion passes directly backwards to the visceral mass and to the metapodium.

* A similar condition of the circulatory system has been observed by Nordmann, Quatrefages, Van Benlden and Allmann, in various Nudibranchiata, though perhaps not quite so distinctly.

Respiratory System.—So delicate a creature would hardly seem to need any special system of this kind, and I found no trace of such organs in any, even the freshest and most uninjured specimens.

In the nearly allied species *Firola Keraudrenii*, however, the gills appear as a row of conical processes, extending along the posterior edge of the body behind the anus; and in other species such processes develope accessory folds, until in *Carinaria* we find fully-formed branchiæ (see EYDOUX and SOULEYET). The ciliated subspiral band (*d*), which will be found to have its homologue in *Atlanta*, is the only structure which appears to be capable of assisting the respiratory function; but its small size must render it of very little importance.

Mantle.—There is no distinct mantle in *Firoloïdes Desmarestii.*

Carinaroides (EYDOUX and SOULEYET) evidently forms the transition from the Heteropods without a mantle to those with one. It is in this genus placed at the lower posterior angle of the body, and carries a minute shell; the branchiæ are developed between it and the anus.

In *Carinaria* there is a proportionably small mantle and shell, but it occupies a position more resembling that of ordinary Mollusks; and in *Atlanta*, as will be seen, the relative proportions of the mantle and body are pretty nearly those found in ordinary Gasteropods.

Contractile Sac or Urinary Organ (*c*, figs. 2, 3).—Between the rectum and the heart, and therefore bathed by the returning venous blood, there lies an elongated, flattened, delicate and transparent sac, whose walls are usually very much wrinkled and sacculated.

This sac opens by a rounded aperture in its upper part upon the right side of the animal, and is of course continually filled by the surrounding water. As the sac is incessantly contracting, however, this water must be continually renewed, and hence the organ, simple as its structure appears and small as its size may be, is probably a very efficient depurating agent*.

Considerations to be stated hereafter, lead me to the belief that it is in fact the urinary organ, at once kidney and urinary bladder.

Reproductive System.—*Firoloïdes* is diœcious. The male may be distinguished at once from the female, by the peculiar penis (*p*) attached to the right posterior inferior angle of the body (fig. 4). It consists of two portions; the larger is cylindrical, but enlarged at its extremity into a globular head, from one side of which a small pointed process projects. The globular body contains many large cells as a sort of lining, and within these there is a cavity which communicates with the exterior through the pointed process. A vast number of small oval fatty-looking particles may be made by pressure to pass out from the cavity.

* In the 'Explication des Planches,' EYDOUX and SOULEYET call a similar organ in *Firola* "organe de la dépuration urinaire ?."

The smaller portion is like a trifid leaf; it is placed at the base of the former portion, and almost reminds one of the sculptor's vine-leaf*.

The *Testis* is not very easily to be distinguished from the liver, behind which it is placed, until the contained spermatozoa are recognized. It occupies about the posterior half of the nucleus. There is hardly any proper vas deferens, but the testis opens by a very short canal at the base of the penis.

The *Ovarium* (*o*) occupies a position similar to that of the testis (figs. 2 and 3). A wide oviduct arises from it about its centre, on the right side, and after making one bend passes downwards, and opens close to the base of the metapodium.

The ovarian ova were oval, about $\frac{1}{300}$dth of an inch in diameter, with a clear, delicate, germinal vesicle about $\frac{1}{600}$dth of an inch in diameter, and a pale, circular, clear, but thick-walled vesicular germinal spot about $\frac{1}{1000}$dth of an inch in diameter. In the oviduct the ova possessed either an entire granular yelk, in which I could not detect any germinal vesicle, or the yelk was broken up into two or more (but not many) spherical or subspherical masses, containing a clear vesicle, the embryo-cell.

In some individuals a long tube (figs. 2 and 5), half as long as the body or more, depended from the orifice of the oviduct. It was colourless and transparent, and appeared as if articulated from its membrane being thrown into regular annular folds.

This egg-tube contained a double series of ova, in which the yelks had undergone division into 8 to 15 masses of very variable size. The ova seemed to have become more divided the nearer they were to the distal extremity of the tube, but I could find none containing a distinct embryo.

The Nervous System (figs. 6 and 7).—Two three-lobed ganglia, closely applied together by their inner edges (fig. 7), are placed between the eyes. Each gives off several branches to the parietes and the following important trunks:—

1. A long branch forwards, which terminates in a small ganglion (β) placed in the angle of union of the œsophagus with the buccal mass, and joined to its fellow by a very short commissure beneath the œsophagus. From these "buccal ganglia" various small nerves are given off forwards to the buccal mass and parts about the mouth, and backwards, to the œsophagus.

2. A large optic nerve (*i*).

3. A nerve to the tentacle.

4. A small nerve from the under surface, which terminates in the auditory sac (*j*).

5. A large and long commissural branch which runs backwards and downwards past the stomach, to unite with the pedal ganglion of its side.

The *Pedal Ganglia* (*y*) are two large ovoid masses in contact by their inner edges.

* According to MILNE-EDWARDS (Sur divers Mollusques, Annales des Sciences, 1842), a perfectly similar penis is found in *Carinaria*. He states, however, that the vas deferens traverses one portion of this organ, which is certainly not the case in either *Firoloïdes* or *Atlanta*.

They give off—

1. Two branches downwards to the propodium.

2. Two branches upwards to the dorsal parietes.

3. Two large branches, which run at first separately below the stomach, and then unite to form a single trunk. This runs along the stomach and intestine, sometimes twisting round them and giving off branches to them and to the parietes; and on the intestine it separates again into two chords, which join two small ganglia (3) placed between the aorta and the intestine; one lies on the aorta, the other between this vessel and the intestine, and they are connected by a commissure. From the former of these ganglia, which is the smaller, two nerves pass upwards and join a flattish mass placed immediately beneath the 'subspiral ciliated band.' There was an obscure appearance of branches radiating from this mass, and it is probably ganglionic.

Organs of Sense. The Eyes (fig. 8).—The eyes are very perfectly organized; each eye is contained within a chamber, excavated in a papilla, whose convex wall forms a sort of supplementary cornea, answering to the cornea of Cephalopoda, or to the corresponding cutaneous cornea of the Gasteropoda.

Their eye-proper is suspended within this chamber by a number of irregular muscular bands, which stretch from it to the walls of the chamber, and perform the function of *oculi-motores*. The optic nerve penetrates the inner wall of the chamber and enters the eye from that side.

The eye-proper is elongated and somewhat hour-glass-shaped, being contracted just behind the crystalline lens. The constriction divides the eye into two portions, an internal and an external. The latter is almost spherical, and is formed by the true cornea, which is much thicker in the middle than elsewhere, so as to present a meniscus section. Behind, the cornea is continuous with the sclerotic coat, which is thick, and seems to be continuous with the neurilemma of the optic nerve.

The crystalline lens is spherical, and is separated by a very small interval from the cornea, so that there is hardly any anterior chamber of the eye. There is no iris, but the inner surface of the posterior chamber is coated by a layer of dark chocolate-coloured pigment*.

The Auditory Vesicles (*j*), fig. 7.—These lie behind and a little below the cephalic ganglia. Each is a spherical vesicle, about $\frac{1}{300}$dth of an inch in diameter. Its walls are irregularly thickened here and there, and it contains a spherical otolithe of about half its diameter. I was unable to perceive any motion in the otolithe. The auditory nerve is a delicate thread arising from the under surface of the supra-œsophageal

* I do not see that the eyes of Heteropoda are so "peculiarly formed" as KROHN has it (Ferner Beitrag zur Kenntniss des Schneckenauges. MÜLLER'S Archiv, 1839). What I have described as the true cornea, is by KROHN considered as an anterior portion of the vitreous humour; such an arrangement would of course be very peculiar, but I think that my account is correct. The eye, it would appear, projects much less in *Carinaria* and *Pterotrachea*; and in the latter, according to KROHN, there is even a rudimentary eyelid.

KROHN does not say anything about the muscles of the eye in these two genera.

ganglion, just in front of the commissural cord. It appears to terminate suddenly on entering the vesicle.

This origin of the auditory nerves from the cephalic ganglia, *when the pedal ganglia are well-marked and placed below the œsophagus,* is a circumstance common to all the Heteropoda*, and, so far as I am aware, altogether peculiar to them among the Mollusca. The only writers who appear to have been struck by it are MM. FREY and LEUCKART: they say that the auditory organs are united with the supra-œsophageal ganglia "only when the lower œsophageal ganglia are wanting (except in *Carinaria,* in which the great length of the lateral commissures of the œsophageal ring appears to have made such a position necessary)." (Beiträge, p. 55.) I must confess I do not see the force of this explanation; and the lower œsophageal ganglia are never "wanting," though they may be united with the upper ones.

II. *Anatomy of Atlanta.* (Plate III.)

This is a very small and very beautiful pelagic mollusk, with a shell not more than one-fourth of an inch in diameter. It appears to be identical with the *Atlanta Lesuerii* of EYDOUX and SOULEYET. Its structure resembles that of *Firoloïdes* in all its essential points, and the transition between the latter and *Atlanta* is complete through such forms as *Firola, Carinaroides* and *Carinaria.*

The shell is flattened and spiral, none of the whorls projecting beyond the plane of the outermost. The aperture is notched on its dorsal edge, and a deep thin crest surmounts the outer whorl, and is generally broken in several places. The surface of the shell is marked by delicate transverse striations.

The outer fourth of the outer whorl of the shell is occupied by the mantle, the rest of the spire containing the viscera.

When protruded, the body of the animal is as large as the shell and appears trifid; the large head forming the anterior division, the "fin" the middle, and the "tail," with its operculum, the posterior division.

The head is large and subcylindrical. Its anterior extremity is formed by a circular lip surrounding the mouth. The eyes are placed far back, and the longish conical tentacles proceed from the anterior part of their base.

The fin or "propodium" (*pp*) is flattened and fan-shaped; its edge is provided with many long and delicate hairs, and its surface is covered with little asperities. Just below its point of attachment, the posterior edge of the propodium carries a cup-shaped disc (*ms*), also fringed with long hairs. This is commonly called the "sucker," and has no representative in *Firoloïdes.* It may be called the *mesopodium.*

The "tail" or *metapodium*† (*mt*) is subcylindrical at its base, but becomes flattened

* Compare MILNE-EDWARDS, Sur divers Mollusques, Annales des Sciences, 1842, and the figures of EYDOUX and SOULEYET, so often referred to.

† That this is the same organ as the metapodium of *Firoloïdes,* will be obvious upon comparing the different forms which it assumes in *Carinaria, Carinaroïdes* and *Firola.*

and acuminated inferiorly. The elongated lanceolate transparent operculum is fixed upon its posterior surface.

The animal moves by the vigorous flapping of its fin. When it withdraws within its shell the head is just retracted, then the fin is folded in, and finally, the tail with its operculum covers up the whole.

The male is distinguished from the female by the presence of a peculiar leaf-like penis (*p*), which is attached upon the right side of the body just above where it divides into the three portions of the foot, fig. 1.

The *Alimentary Canal* commences above an oval buccal mass, widens gradually into the stomach, then narrows again and opens into a quadrangular sac, which communicates with the liver. From the anterior and upper part of this sac the rectum is continued and runs forward to the upper and dorsal part of the branchial cavity, in which it terminates by a tubular anus.

The mechanism of the tongue exactly resembles that of *Firoloïdes*. Two long cylindrical salivary glands (*f*) open into the anterior part of the œsophagus. They are simple cæca lined by a thick epithelium.

The *Liver* (*l*, fig. 3) is a wide conical sac with sacculated and glandular walls; its communication with the quadrangular dilatation of the intestine is so wide that it may almost be considered as a diverticulum thereof, and it extends back as far into the spire of the shell as any of the viscera.

The rectum is of a pinkish colour, and is richly ciliated internally.

Circulatory System (figs. 2, 3, 4).—The heart resembles that of *Firoloïdes*, and consists of an auricle (*u*) and a ventricle (*v*). It lies parallel to the rectum, with the auricle forwards at the base of the mantle-cavity, and the animal is therefore prosobranchiate. The aorta proceeds from the apex of the ventricle, and immediately after its origin divides into two branches, one of which runs backwards to the visceral mass, while the other passes forwards close beneath the stomach, until it terminates in the buccal mass. After passing over the subœsophageal ganglia, it gives off a downward branch to the fin, but I did not observe the peculiar termination of this artery which obtains in *Firoloïdes*; this perhaps may be accounted for by the greater muscularity of the fin in *Atlanta*, rendering it less transparent. The venous blood has no distinct channel, but returns to the heart by the cavity of the body. The returning current of blood-corpuscles is very obvious; they seem to pass quite freely in all directions round the intestine, aorta and nervous centres, the general tendency being always backwards towards the heart.

Respiratory System.—Very distinct gills are figured by Eydoux and Souleyet in most Atlantæ, but their presence in this species was decidedly exceptional, the majority of specimens presenting no trace of them. Once I noticed a bundle of long branchial filaments depending from the wall of the mantle-chamber; and in another case rudimentary and undeveloped short processes of the same kind were to be seen; they contained canals, through which a small portion of the returning venous blood was diverted, fig. 4.

The *Mantle* is very well developed; a peculiar thickened and ciliated band crosses it transversely, and seems to be the homologue of the subspiral ciliated band in *Firoloïdes* (*d*).

Contractile Sac.—This resembles the corresponding organ in *Firoloïdes*; it lies between the rectum and the heart, and opens into the bottom of the chamber of the mantle by a well-defined oval aperture, figs. 3 and 4 *c*.

Generative Organs.—The ovary or testis is an elongated mass corresponding to the liver, and occupying the inner and right half of the visceral mass, fig. 3 *t*.

The *Ovary* consists entirely of a mass of ova in course of development, with their characteristic germinal vesicle and spot. The oviduct commences at its anterior larger extremity; it is very wide and passes forwards, forming many convolutions, and terminates in the mantle-cavity by the side of the anus.

The *Testis* contains a mass of small cells and spermatozoa in various stages of development. The vas deferens leads from its anterior extremity, and before terminating in the cavity of the mantle, dilates, occasionally forming thus a dark spherical vesicula seminalis, *s*, fig. 3.

There is a kind of penis attached to the right side of the neck of the animal just above the foot (*p*, fig. 1): it is composed of two portions arising from a common base. The anterior and inner is like a three-pointed leaf; a cæcal ciliated canal runs along its centre. The posterior portion is a tubular cylindrical process, with a kind of ciliated cup at its extremity (fig. 5): a conical body projects into this below. The tube is nearly filled with small oval granules. The resemblance between this and the penis, which has been described in *Firoloïdes*, cannot be misunderstood, and the position of the organ in *Atlanta* corresponds with that in *Firoloïdes*, if we consider the left filamentous process in the latter to be the metapodium. That it is so, is demonstrated not only by the distribution of the metapodal arteries, but by an examination of the intermediate genera above mentioned.

Nervous System (figs. 2 and 6).—This consists of two trilobed supraœsophageal ganglia (fig. 6), which correspond to those of *Firoloïdes*, and give off similar nerves; but in addition their posterior lobes give off each a long nerve*, which runs back upon the stomach, and below its posterior narrowing, between this and the aorta, joins with its fellow in a small ganglion (not figured by EYDOUX and SOULEYET); some branches pass from this to the viscera, and two or three run in the substance of the mantle to the "ciliated band," fig. 4.

The commissural cords which unite the supraœsophageal with the subœsophageal or pedal ganglia, are at first double (fig. 6), but afterwards unite into one. They are connected with the subœsophageal or pedal ganglia (*y*), two large oval masses from which several branches are given to the different parts of the foot; and each gives off one long cord which runs along the lower surface of the intestine, and probably joins the ganglion upon the aorta before mentioned.

* In *Carinaria* a similar commissural nerve, between the cephalic and the parieto-splanchnic system of ganglia, has been shown to exist by MILNE-EDWARDS (*loc. cit.*), but I could find none in *Firoloïdes*.

The *Eyes* (*i*, fig. 6) resemble those of *Firoloïdes*, except that their pigment is black.

The *Auditory Vesicles* are spherical and about $\frac{1}{380}$th of an inch in diameter. Each contains a single strongly refracting globular otolithe of about $\frac{1}{800}$dth of an inch in diameter. In some cases this had a slow movement of rotation upon its axis, fig. 6, *j*.

Now in regarding *Firoloïdes* and *Atlanta*, whose structure has just been described, as illustrations of a typical form, the following circumstances appear to me to be of importance:—

1. The intestine is bent dorsad, or towards the side on which the heart is placed. The visceral mass is situated below and behind the posterior portion of the alimentary canal; it may be called a post-abdomen.

2. *Atlanta* is prosobranchiate; *Firoloïdes* is neither opisthobranchiate nor prosobranchiate.

3. The foot consists of three parts, the propodium, mesopodium and metapodium, in *Atlanta*; but of these the mesopodium disappears in *Firolöides*, and the metapodium becomes very rudimentary.

4. The auditory organs appear to be connected with the cephalic ganglia.

5. The animals are unisexual.

III. *Anatomy of Pteropoda.* (Plate IV.)

The variation of form undergone by the members of this group is perhaps greater than that which takes place in any other, except it may be the Nudibranchiata, and hence their structure is particularly instructive.

Three very distinct modifications of the type present themselves at first sight. The first is characterized by the non-development of the mantle and the full development of the foot, ex. *Pneumodermon, Clio*, fig. 1.

The second, by the great development of the mantle, by its cavity opening upon the ventral surface, and by the minuteness or absence of the mesial portion of the foot, ex. *Cleodora*, fig. 4.

The third resembles the second, but the mantle-cavity is placed upon, or at any rate opens upon the dorsal surface, ex. *Spirialis, Limacina.*

1. It is very remarkable that Cuvier should not have recognized in the "espèce de menton," and the "deux petits lèvres*" of *Pneumodermon*, nor in the "deux tentacules triangulaires" of *Clio*†, the homologues of the foot of the Gasteropoda. In fact it was on the strength of their having no such appendage that he founded his new order of Pteropoda‡, and yet the resemblance of the inter-alar appendages in these two genera§ to the foot of Gasteropods is so striking as at once to point to their real nature.

* Mém. sur le Pneumoderme, p. 7.

† Mém. sur le Clio, p. 6.

‡ Mém. sur le Clio, p. 9; sur l'Hyale et le Pneumoderme, p. 10.

§ This is fully recognised by Leuckart, "Ueber die Morphologie," &c. p. 149.

In truth, the foot, though very small in these genera, is exceedingly well-marked, and shows a clear division into mesopodium and metapodium. It may be a matter of doubt whether the propodium is developed or not, and this question can be settled by embryology alone; but for the present, I think, it may be fairly presumed that it is represented by the tentaculigerous hood of *Pneumodermon* and by the tentaculigerous lobes of *Clio*; following in this case a very common tendency (exemplified in all the Cephalopods and in many Gasteropods) to become developed over and in front of the mouth*.

As CUVIER demonstrated, there is no "mantle" in *Pneumodermon* and *Clio*†; the body of these mollusks answering precisely to that of a *Firoloïdes*. The relation of the gill-laminæ and of the small anomalous shell in *Pneumodermon* sufficiently corroborates CUVIER's view. Gills are never placed upon the outer surface of a mantle; and if anything answers to such an organ it must be the small space covered by the rudimentary shell, so that the relations of the parts are, in fact, similar in *Pneumodermon* to what we find in *Firola* and *Carinaroïdes*.

Finally, new parts, the "alæ," make their appearance in these genera and give its character to the order (figs. 1, 2, 3, 4, 7, *ep*).

Considering the position and relation of these organs as distinct developments from the upper part of the sides of the foot, and the fact that their nerves arise, like those of the foot, from the pedal ganglia, I propose to consider them as parts of the foot and to call them the "epipodia." It has been long since shown by VAN BENEDEN and others that they have nothing to do with the respiratory function.

In this subtype the intestine opens on the right ventral side of the neck, and dissection shows its first bend to be ventral, that is, towards the side of the pedal ganglia.

2. The genus *Psyche*‡ or *Euribia* offers a very interesting transition from the foregoing to the second subtype. This genus is commonly said to have a cartilaginous shell, but this so-called shell appears, upon careful examination, to be only the thickened integument of the body; it is not secreted by a true mantle, like that of *Cleodora*, &c. The notion of a shell has arisen seemingly from the fact that a sort of cleft exists anteriorly from which the locomotive organs of the animal can be protruded and into which they can be retracted, but at the margin of this cleft the softer

* The origin of the nerves of the acetabuliferous tentacula may probably throw some light upon this matter; I have not had the opportunity of dissecting sufficiently large specimens of either *Pneumodermon* or *Clio*, carefully, with regard to this especial point. From the figures of EYDOUX and SOULEYET, one would be led to believe that the nerves of the acetabuliferous tentacles arise from the cephalic ganglia, which would be a very great objection to the view advocated above, since all the other parts of the foot, the mesopodium, metapodium and epipodium are supplied by the pedal ganglia. (See EYDOUX and SOULEYET, plate 15. fig. 30, and plate 15 bis, fig. 8.)

† EYDOUX and SOULEYET, however, call it "manteau" in the description of their figures. LEUCKART also opposes CUVIER's view, but I think without reason. (*Op. cit.* p. 146 note.)

‡ My species appears to be the *Euribia Gaudichaudii* of EYDOUX and SOULEYET.

parts of the body are continuous with the harder, just as the body of a Polyzoon is connected with its cell.

In some individuals I have observed the posterior extremity of the body to be surrounded by two circlets of cilia*.

The head of the animal is provided with two very large tentacles†, which carry a large process upon the inner side of their base, and rudiments of eyes upon the outer. Between the tentacles on the ventral side are two projecting lips with the aperture of the mouth between them, fig. 3.

Behind the mouth there are two lobes, separated by a deep notch; these are the two portions of the mesopodium which had begun to be separated in *Clio*. Behind these, again, there is a single tongue-shaped lobe, the metapodium, which is continuous on each side with two elongated and expanded epipodia.

There are no gills, and the anus opens ventrally upon the left side.

From this genus, to that called *Criseis* by RANG, but which EYDOUX and SOULEYET unite with *Cleodora*, the transition is very easy, figs. 6, 7.

In these forms there is an elongated conical shell, narrow and straight, or wider and slightly curved at its extremity. The body puts one in mind of that of a Cephalopod, being enveloped in a wide mantle, which is united to the body on the dorsal side only (fig. 6). The wall of the mantle is very thick, so that it presents a wide aperture always open upon the ventral side. Its free edge is, as it were, cut down upon its dorsal side, so that ventrally it is considerably longer. On the right side this prolonged portion has a rectangular edge, but upon the left it forms a sort of ram's-horn process‡. The lower part of the inner surface of the mantle is richly ciliated, and is raised into a number of transverse ridges, which must probably be considered to be rudimentary gills.

The head and wings are united with the part of the body covered by the mantle, by a narrow neck; compared with *Euribia*, the change in form is such as would be produced by a lateral expansion of the foot. Behind the mouth is the wide metapodium, and on each side of it are the broad epipodia continuous with the metapodium. About midway between the mouth and their margin the epipodia carry a small triangular lobe (*ms*), which evidently represents one-half of the mesopodium; and nearly at the same level, on their anterior edges, they present two small curved and pointed processes, the representatives of the large tentacles of *Euribia*. Two minute papillæ, the rudiments of the eyes, are placed upon the dorsal surface just behind the anterior edge of the alæ (*i*).

* It is a very interesting fact that Professor MÜLLER has found the larvæ of *Pneumodermon* to be provided with similar ciliated bands, Ueber die Entwickelungs-formen, &c. Monatsbericht d. k. Akad. d. Wiss. zu Berlin, October 1852.

† These are called "branchies" by EYDOUX and SOULEYET (pl. 15.), but why I cannot divine, since these organs are certainly homologous with the tentacles of *Cleodora*.

‡ Is this to be compared with the small posterior curved process of the edge of the mantle in Gasteropteron?

The œsophagus takes a straight course backwards from the mouth, which contains a minute lingual prominence, and widens gradually into a pyriform muscular gizzard, which is provided with two strong curved and conical teeth. The intestine passes from the narrow pylorus, and preserving the same width throughout, bends downwards towards the ventral side, and ultimately terminates in the cavity of the mantle a little to the left of the mesial line, fig. 6.

Just behind the pylorus a very long straight cæcum is given off, and sometimes there is a short one in addition by the side of it. The parietes of these sacs are glandular.

A long "columellar" muscle attaches the animal near to the apex of its shell, and then passes down into the foot, where it spreads out.

The position of the heart varies remarkably in this genus, and this variation is still more remarkable, if, with EYDOUX and SOULEYET, we consider it to be one with *Cleodora*.

In *C. aciculata* (figs. 6, 7) the mantle-cavity extends considerably beyond the transversely-barred portion of the mantle, and the base of the auricle abuts upon its lower posterior portion. The apex of the heart points backwards and a little to the left side, and in M. MILNE-EDWARDS's arrangement the animal would be prosobranchiate. In *C. virgulata* (E. and S.) the base of the auricle lies behind the right posterior portion of the mantle-cavity, and the apex of the ventricle points directly to the left; it is therefore neither prosobranchiate nor opisthobranchiate.

In *Cleodora curvata*, on the other hand, as will be seen immediately, the base of the auricle is posterior and the ventricle points forwards; it is opisthobranchiate, figs. 4 and 5.

In this one genus, then, we have every transition from the prosobranchiate to the opisthobranchiate type of organization.

The aorta is too delicate to be readily traced in *C. virgulata* and *C. aciculata.* It may however be seen passing through the nervous ring and bifurcating for the epipodia, fig. 7 *w*. There is no rudiment even of a venous system.

The *Cleodora curvata* (figs. 4 and 5) (one of the true *Cleodoræ* as formerly defined) forms a transition from the preceding species to *Hyalæa*. It has the general organization of the former, with the flattened shell more or less fissured laterally, and the filiform appendages to the mantle, of the latter.

The alary expansion forms a more rounded disc than in *C. aciculata* and *virgulata*, the metapodium having become widened out and almost undistinguishable from the epipodia. The triangular lobes, rudiments of the mesopodium, have disappeared.

The intestinal canal resembles that of the two former species; its flexure is ventral, and the anus opens into the cavity of the mantle on that side. The long cæcum has orange-coloured glandular parietes.

The position of the heart has been described. It is comparatively large, and the aorta may be readily traced from it, passing forwards over the stomach and through

the nervous ring, and eventually dividing into two branches, one for each epipodium.

There is a more distinct rudiment of a venous system in this mollusk than in *Firoloïdes* or *Atlanta.* A wide canal traverses the mantle towards its upper part; it is crossed by various muscular bands. Another distinct canal can be traced from the auricle towards the right side, skirting the lower border of the branchial chamber. Whether it becomes continuous with the right extremity of the previous canal or not, I could not certainly determine. The blood flows from both ends of the first-mentioned canal towards the auricle, but on the left side there does not appear to be so distinct a venous canal as on the right.

In all species of *Cleodora* there is an elongated sac, in its structure, contractions, and position relatively to the heart, exactly resembling that of the Heteropoda. It communicates by a small aperture with the cavity of the mantle.

The *nervous system* in all these species consists of three ganglia on each side of the œsophagus. Four of these form a mass, placed entirely below the œsophagus, and the other two, placed in contact with and immediately above them at the side of the œsophagus, are united above by a broad flattened supraœsophageal commissure.

The upper (*cephalic*) ganglia give off two principal branches to the rudimentary eyes and tentacles. The anterior pair of the lower mass (the *pedal* ganglia) give off branches to the epipodia and expansion of the foot generally; posteriorly they carry two small auditory vesicles, with many otolithes.

The posterior (*parieto-splanchnic**) ganglia give off their principal branches to the mantle.

The aorta passes between the pedal and parieto-splanchnic ganglia.

3. I have mentioned that a third subtype appears to be formed by *Spirialis* and *Limacina*, which are the only Pteropods with spiral shells. *Spirialis*, again, is the only Pteropod with an operculum. But a more important difference for my present purpose consists in the fact, that in these genera the mantle-cavity (and with it the anus) opens on the dorsal side of the animal. I have not myself been fortunate enough to obtain specimens of these genera, and as the attention of those anatomists who have examined them does not appear to have been specially directed to this point, it is impossible to make out with certainty whether the first flexure of the intestine is also dorsal, or whether, as in all other Pteropods, it is ventral. I cannot think that any real variation will be found to occur among closely allied forms, in a matter so fundamentally connected with their whole structure and mode of development; and I would suggest that here also the bend of the intestine is truly ventral, but that by a continuation of the process by which the anus is thrown to the left side in *Cleodora* and to the right in *Pneumodermon*, it (with the branchial cavity) is thrown to the dorsal side in *Limacina* and *Spirialis*. Such a change would be completely paralleled by the arrangement of the parts in the Ascidians, where the first bend of the intestine is dorsal; but the cloaca, which corresponds to the mantle cavity, opens on

* See below, p. 54.

the ventral side, carrying the anus with it; and even in other Pteropoda we find changes in the arrangement of the mantle-chamber, which to a great extent modify, without however essentially altering, the normal arrangement, *e. g.* in *Hyalæa* and *Cymbulia,* where the posterior extremity of the mantle-chamber extends up to the dorsal surface.

Furthermore, the position of the heart, which remains on the ventral side in *Spirialis* (E. and S., plate 11. p. 13, &c.), greatly strengthens this view of the case.

Leaving this question in abeyance until further light is thrown upon it, we may, I think, enunciate the following propositions with regard to the Pteropoda corresponding to those in which the organization of the Heteropoda was summed up:—

1. The intestine is bent towards the ventral side; the visceral mass is placed above, and in front of the anus; it may be called an abdomen.

2. Some Pteropoda are prosobranchiate, others intermediate, others opisthobranchiate.

3. The foot consists of four parts:—three, the propodium, mesopodium, and metapodium, such as are found in the Heteropoda; and a fourth, the epipodium, not found in the Heteropoda. All of these parts (propodium?) may be distinguished in *Pneumodermon* and *Euribia,* while all but the epipodium and metapodium have disappeared in *Cleodora.*

4. The auditory organs are connected with the pedal ganglia.

5. The Pteropoda are hermaphrodite*.

PART II.

The Heteropoda and Pteropoda, whose anatomy I have just endeavoured in a very general way to sketch and illustrate, may be regarded, in some respects, as opposite poles of the development of the archetype of the Cephalous Mollusca. We have now to consider what that archetype is, and by what process it has become modified into the actual forms which have been described; and with the solution of these questions is connected the meaning and justification of certain new terms of which I have made use.

The most proper way of proceeding in this matter would of course be, to trace the *development* of the Heteropoda and Pteropoda. Unfortunately, however, I have had no opportunity of doing this myself; and so far as I am aware, there is no account of the embryogenesis of Mollusks belonging to either of these classes extant†.

* This, it will be observed, is here stated for the first time. In the Heteropoda the nature of the generative system has been a matter of controversy, and I therefore gave an account of it at length in *Firoloïdes* and *Atlanta.* The hermaphrodism of the Pteropoda, on the other hand, is well-known, and a description of their generative organs would only have led to details without any morphological bearing.

† Since the above paragraph was written, this hiatus has been filled, so far as the Pteropoda are concerned, by Vogt (Bilder aus dem Thierleben, p. 289) and by Johannes Müller (Ueber die Entwickelungs-formen einiger niedern Thiere. Monatsbericht d. k. Akad. zu Berlin, October 1852).

But in any natural group of animals the grand laws of development and growth are so uniform (the uniformity in fact constituting the true bond of union of its members), that this want may be supplied by the very full information we possess with regard to other Mollusca. If from these data certain general propositions can be established, it will, I think, be perfectly fair to make these propositions the basis whence deductively to explain and account for facts of organization whose absolute genesis is not known.

The development of the Cephalopoda, Pulmonata, Nudibranchiata, and Tectibranchiata, has been very carefully made out by Kölliker, Van Beneden and Windischmann, Schmidt, Gegenbaur, Sars, Nordmann, Vogt, Reid, and others. From their observations the following generalizations may be very safely made.

1. The development of a Mollusk commences on the hæmal* side, and spreads round to the neural side, thus reversing the process in Articulata and Vertebrata.

2. In all Mollusks the axis of the body is at first straight, and its parts are arranged symmetrically with regard to a longitudinal vertical plane, just as in a vertebrate or an articulate embryo†. Plate V. fig. 1.

3. The subsequent bent, spiral, or otherwise unsymmetrical arrangement of the parts of the body in Mollusca, depends upon the development of one part at the expense of, or disproportionately to, another; and this asymmetrical over-development never affects the head or the foot of a Mollusk, but only a portion, or the whole of the hæmal surface. Plate V. figs. 2–8.

4. It is to this portion, and its often free projecting edges, that we can alone properly apply the term "*mantle*." When this outgrowth takes place before the anus, I propose to call it an *abdomen*; when it takes place behind the anus, a *post-abdomen*.

5. All embryological evidence goes to show that the Cephalopoda and Pulmonata develope an *abdomen*. The intestine becoming drawn into the abdominal sac becomes in consequence bent towards the neural side. Plate V. figs. 2–5.

6. On the other hand, all the evidence hitherto obtained with regard to the de-

* This very remarkable law has not, it appears to me, received its due importance at the hands of those distinguished anatomists, Kölliker (for the Cephalopoda), Van Beneden and Windischmann and Gegenbaur (for the Pulmonata), Vogt (for the Nudibranchiata), and Leydig (for the Pectinibranchiata), from whose observations I deduce it. Vogt, however, observes that the order of appearance of organs in the Mollusca is the inverse of that in the Vertebrata; and with regard to the point from whence development commences, he says, "Ce point est facile de trouver, il est situé en arrière des roues a peu près sur la ligne de jonction entre la partie céphalique et la partie ventrale, et même un peu en arrière de cet dernière sur la partie abdominale même," p. 39.

I use the terms *hæmal* and *neural* here to avoid the ambiguity of dorsal and ventral, which have opposite meanings when applied to the Vertebrata and the Invertebrata. The hæmal side is that upon which the vascular centre is developed, it is the dorsal side of Articulata, the ventral of Vertebrata. The neural side is that upon which the nervous centres are developed; it is the dorsal side of Vertebrata, the ventral of Invertebrata.

† "Instead of the radial type of development we meet quite unmistakeably with a lateral symmetrical type; instead of the extended form of the body we find a short compressed body without repetition of segments or lateral appendages."—R. Leuckart, Morphol. p. 125.

velopment of the Nudibranchiata, Tectibranchiata and Pectinibranchiata, tends to the conclusion, that in them the visceral mass is thrust out *behind* the anus; is in fact a *post-abdomen**. Plate V. figs. 6–8.

A little consideration will show that the intestine drawn into this must become bent towards the *hæmal side*, as in fact it is in the embryos of all three groups†.

Upon embryological grounds, then, we should establish two great primary modifications of the molluscous archetype; the one characterized by the development of an *abdomen*, and a consequent *neural* flexure of the intestine; the other marked by the development of a *post-abdomen*, and the consequent *hæmal* flexure of the intestine.

But these modifications of anatomical structure exactly correspond with those which I have already demonstrated, upon anatomical grounds, to occur in the Pteropoda and Heteropoda; and I trust I am not overstepping the bounds of legitimate analogy in assuming that the anatomical fact of a neural flexure indicates the embryological development of an abdomen; that of a hæmal flexure, the development of a post-abdomen; and that therefore the Pteropoda fall into the same category with the Cephalopoda and Pulmonata; the Heteropoda into that of the Pectinibranchiata, Tectibranchiata and Nudibranchiata.

It is remarkable, that, as regards the flexure of the intestine, similar contrasted modifications of the archetype take place in those animals which are the nearest allies of the Mollusca; I mean the Ascidians and Polyzoa, the Molluscoïdes of Milne-Edwards. In each of these groups the intestine is always bent upon itself; but while in the Ascidian the bend is always *hæmal*, in the Polyzoon it is *neural*. The latter fact is evident to any one who will examine a Polyzoon; the former may seem at first sight to be contradicted by the circumstance, that the ganglion in the Ascidians is placed between the cloacal and branchial apertures. However, as I have endeavoured to show elsewhere‡, whatever be the position of the anus in the Ascidians, the first bend of the intestine is always hæmal. I have already referred to their probable analogy with *Spirialis* in this respect.

Having now determined the changes which take place in the axis of symmetry of the Mollusca, let us examine into those undergone by their principal external organs.

Whether we have to do with a Cephalopod or with an ordinary Mollusk, the first step in development is the separation of the blastoderm into a central elevation, the

* See particularly Leydig, *Ueber Paludina vivipara*, Siebold and Kölliker's Zeitschrift, 1850, where the thrusting forwards of the anus by the development of the mantle is particularly shown, p. 142.

"A considerable change in the position of the anus takes place when the fold of the mantle becomes formed and moves forward, because thereby the intestine and anus are also thrust forward, and to the right side."

† The development of the Pectinibranchiata cannot be said to have been carefully worked out yet, with the exception of that of *Paludina*, but what has been done tends to the conclusions above stated.

‡ Upon the Anatomy and Physiology of *Salpa* and *Pyrosoma*, Philosophical Transactions, 1851, and in a "Report upon the Structure of the Ascidians," read before the British Association, September 1852. The law as regards the Polyzoa was first enunciated by Professor Allman, "On the Homology of the Organs of the Tunicata and Polyzoa," Trans. Royal Irish Acad. vol. xxii.

mantle, and certain lateral portions. Now these portions become in the Gasteropoda, the head and foot; in the Cephalopoda, the head and arms. It follows therefore that the arms of the Cephalopod are homologous with the foot of the Gasteropod.

Again, in the Cephalopod an eminence becomes developed along two lines, which run on each side of the upper part of the "lateral expansions" and meet behind the head; along the anterior portion of this line the eminence remains as a slight ridge, which afterwards becomes one of the muscles of the funnel; along the posterior portion of the line a considerable process is developed, and, uniting with its fellow, becomes the funnel.

In the Gasteropod, it is along the *anterior* halves of two corresponding lines that processes are developed, which become the ciliated alæ or vela of the embryo. The line in question I propose to call the *epipodial line,* and whatever is developed along that line I consider to be the epipodium, or a portion of it. I do not venture upon such a refinement at present, but I think it *probable,* that as we have distinguished three portions in the foot, so it will be necessary to distinguish three portions in the epipodium; anterior, middle and posterior. For instance, in the Cephalopoda the posterior portion only is developed as the funnel; in the Gasteropod larvæ the ciliated vela are the homologues of its anterior portion. The palmated lobes of the Turbinidæ, the "lobes of the mantle" of *Aplysia,* appear to be developed from the whole epipodial line, while it is apparently the middle epipodium alone which is developed into the "wings" of the Pteropoda.

All traces of the epipodium appear to have vanished in the majority of the Pectinibranchiata*.

Of all mollusks *Atlanta* possesses the best developed *foot*-proper, and has its parts

* Leuckart and Lovén have enunciated very different views with regard to the homologies of the external organs of the Mollusca, to which it seems proper I should refer.

Leuckart, for instance (*op. cit.* pp. 155–59), considers that the anterior cephalic lobes of the embryo Cephalopod answer to the cephalic velum of Gasteropoda; the posterior cephalic lobes to the alæ of Pteropoda, while the funnel corresponds with the middle lobe of the foot. The arms he considers to be peculiar structures, mere appendages to the cephalic lobes.

If the halves of the funnel, however, answer to the middle lobes of the foot, how is it that they unite upon the dorsal surface of the neck? If the anterior cephalic lobes answer to the vela of Gasteropoda, how is it that the latter disappear, and do not contribute to the formation of the head in Gasteropoda? Finally, it must be remembered that the arms of the Cephalapoda arise quite independently of the cephalic lobes, the first developed arms being those most distant from the head.

Leuckart considers that the oral lobes of the pulmonate embryo are the homologues of the ciliated vela of Gasteropoda. But their position and number are against this view. It seems to me that these oral lobes correspond with the cephalic lobes of the embryo Cephalopod, and it has been well shown by Gegenbaur (*op. cit.*) that the whole so-called "yelk-sac" of the Pulmonata is the true homologue of the vela in Pectinibranchiata; the "ciliated bands" of Van Beneden and Windischmann turn out to be Wolffian bodies, and to be *internal,* not external organs.

The common view, that the alæ of the Pteropoda are the persistent vela of the embryo, is, so far as I am aware, unsupported by any evidence. Embryology teaches us hitherto that the anterior part of the epipodium

best specialized and separated. In the special description of *Atlanta* names have been given to these parts, whose appropriateness is I hope obvious.

From this highly developed condition of the foot, to its diminished state in *Glaucus* and its total absence in *Phyllirrhoë*, we have every gradation. The various portions are still to be distinguished in *Pteroceras* and the *Strombidæ*, but lose their distinctness for the most part in other Gasteropoda. However, the propodium is still marked off by a transverse fissure in *Oliva* and *Ancillaria*, and attains a great development in size; a peculiarity which is still more remarkable in *Natica* and *Sigaretus*. In both these genera it shows a tendency to invest the head. In the Cephalopoda, the anterior arms, which must be considered as the propodium, fairly unite in front of the mouth, and it seems very possible that the cephalic hood of *Gasteropteron*, the "oral" tentacles of *Aplysia*, the hood of *Tethys*, the "lips" of some Pteropoda, and the hood of *Pneumodermon* may be the result of a similar change. But all attempts to settle these points, save by development, must be more or less hypothetical*.

To this same test of development we must refer everything which claims to be called "*mantle*," a word which has perhaps been more vaguely and loosely used than any other term in zoology. Surely if a term is to have any value in either zoological or anatomical nomenclature it must be applied to only a defined thing. The "mantles" of a *Sepia*, a *Cleodora*, or a *Buccinum* may be homologous with one another, but they certainly are not so with what is called the "mantle" in *Doris* or any other Nudibranch†. The simple fact that the cephalic tentacles arise in the midst of the

is never permanently developed, and the position of the alæ would lead to the belief that they correspond to its lateral portions[1].

So far as I can judge from the Latin table affixed to his Swedish essay on the development of the Acephala, LOVÉN considers the arms of the Cephalopoda, the three pairs of cephalic tentacles of *Clio*, and the cephalic lobes of *Tethys*, to be homologous with the velum of the Gasteropod embryo, while the funnel of Cephalopoda and the alæ of Pteropoda are homologous with the foot of Gasteropoda.

The considerations above cited appear to me to furnish a sufficient refutation of these views, which seem to be the offspring of an idea first propounded by their learned author in his "Contributions to the Embryology of the Mollusks" (OKEN's Isis, 1842), that the hood of *Tethys* and the cephalic processes of *Tergipes* are modifications of the cephalic vela of the embryo. This ingenious hypothesis has not however been confirmed by observation so far as regards *Tethys*, and has been directly *dis*proved with respect to *Tergipes* (see SCHULZE, Ueber die Entwickelung d. *Tergipes lacinulatus*, WIEGMANN's Arch. 1849).

* In the absence of any knowledge of development perhaps the source of the nervous supply is one of the best tests of the real homology of a part. Mr. HANCOCK, in his valuable paper "Upon the Olfactory Apparatus in the *Bullidæ*" (Annals of Nat. Hist. March 1852), has, I observe, applied this test to the cephalic expansion of the *Bullidæ*, to the hood of *Gasteropteron*, &c.; and since it clearly appears that these parts are supplied by nerves from the *cephalic* ganglia, which never give branches to any portion of the foot, the suggestion in the text must be given up.

† LEUCKART, believing the hæmal tegument of the Nudibranchiata to represent a mantle, suggests that there

[1] The researches of VOGT, already referred to, have fully confirmed this conclusion. The embryo Pteropod has vela, which eventually disappear, while the epipodia are developed quite distinctly from the upper part of the sides of the "foot."

so-called "mantle" of the latter, is sufficient evidence to show that it cannot be homologous with the "mantle" of the former. The so-called "margins of the cloak" in these genera appear to me to have much more relation to the epipodium.

Cuvier allows a mantle to *Doris*, but denies it to *Glaucus* and *Eolidia*; why, is not obvious.

Leuckart defines a mantle to be "a scutellate (schildförmig) duplicature of the outer integument extending from the neck for a varying distance backwards." By this definition however the upper surface of the anterior division of a *Bulla* would be a "mantle," which it is not, since the true mantle is obviously behind separated from this by a deep cleft, and how would the mantle of *Firola* or *Carinaroides* answer the definition?

If the definition which I have given of the true "mantle" be correct, we must, I think, hesitate for the present in conferring that name upon the dorsal shell-bearing integument of *Chiton*. May this not be homologous with the thick-edged dorsal surface of a *Doris*, in which the calcareous particles instead of being scattered are united into distinct plates*?

With regard to the shells, again, at the risk of being blamed for over-refinement, I would suggest, that it is, to say the least, an open question, whether the shell of *Buccinum* is (as it is commonly supposed to be) homologous with that of *Helix*; that of *Sepia* with that of *Nautilus* and *Ammonites*; that of the embryo *Aplysia* with that of the adult *Aplysia*. Grave differences of development occur in some if not in all of these cases†.

is a difference between their "gills" and those of other Mollusks, which, as he justly observes, are never processes of the mantle, *loc. cit.* p. 130. The argument in the text tends to show, that in this respect there is in reality no difference between the "gills" of the Nudibranchiata and those of other Mollusks. On other grounds however I am inclined to think that Leuckart's distinction is a just one. The organs called gills in the Nudibranchiata appear to me to be in all cases what they undoubtedly are in *Eolis*, viz. gastro-hepatic appendages. Even in *Doris*, where they are gill-like, they are supplied with hepatic blood only. See Hancock and Embleton's admirable memoir "On the Anatomy of *Doris*," Philosophical Transactions, 1852.

* In D'Orbigny's genus *Villiersia*, allied to *Doris*, the calcareous tegumentary particles of the *Doridæ* have united into a flat shell, hidden in the "mantle," which is pierced by the apertures for the tentacles and gills. The disposition of the calcareous particles in the *Doridæ* is very regular, though it seems too much to assume with Lovén that they imitate a subspiral shell (see Lovén, Oken's Isis, 1842).

† The memoir by Dr. Gegenbaur, "Beiträge zur Entwickelungsgeschichte der Land Gasteropoden," which has just appeared in Siebold and Kölliker's "Zeitschrift für Wissenschaftliche Zoologie," furnishes very powerful support to the doubts above suggested, since it demonstrates that the shell of *Clausilia*, and gives good reason for believing that that of *Helix*, are developed within the substance of the mantle, following exactly the type of *Limax*.

"The land Gasteropoda are distinguished by the peculiar mode of development of their shell, if we may draw conclusions for the whole group from *Helix* and *Clausilia*. The original deposition of the shell in the interior of the mantle (as in the *Loligidæ* among the Cephalopoda) is as yet an isolated fact among the land Gasteropoda, of which we find no indication in other Gasteropods."

There seems to be a very curious relation between the internal or external nature of a shell, the curvature of its whorls as regards a vertical plane, and the hæmal or dorsal flexure of the intestine.

Take, first, the case of a true external shell, as that of *Nautilus* or *Argonauta*, or *Atlanta*. Here the direction

From all that has been stated, I think that it is now possible to form a notion of the archetype of the Cephalous Mollusca, and I beg it to be understood that in using this term, I make no reference to any real or imaginary "ideas" upon which animal forms are modelled. All that I mean is the conception of a form embodying the most general propositions that can be affirmed respecting the Cephalous Mollusca, standing in the same relation to them as the diagram to a geometrical theorem, and like it at once imaginary and true.

The archetype of the Cephalous Mollusca, then, it may be said, has a bilaterally symmetrical head and body. The latter possesses on its neural surface a peculiar locomotive appendage, the foot; which consists of three portions from before backwards, viz. the propodium, the mesopodium and the metapodium, and bears upon its lateral surface a peculiar expansion, the epipodium (Plate V. fig. 1).

The hæmal surface of the archetype may or may not secrete a shell upon its surface, or in its interior.

If we compare this unmodified form with the vertebrate or articulate archetype, we find that the three essentially correspond. The appendicular system of the Vertebrata and Articulata is represented by the epipodium in the Cephalous Mollusca (Plate V. figs. 9, 10, 11).

Nevertheless the differences between the three archetypes are so sharp and marked, as to allow of no real transition between them.

In the Cephalous Mollusca *it is the hæmal side of the body which is first developed.* In the Articulata and Vertebrata it is the *neural side which first makes its appearance.*

The archetype of the Cephalous Mollusca further differs from that of the Vertebrata (and resembles that of the Articulata), in the circumstance, that while in the latter the nervous and intestinal axes are parallel, in the former they decussate; that is, the œsophagus opens on the neural side, passing between the great nervous commissures.

The molluscous archetype again differs from that of both Vertebrata and Articulata in its appendicular system (*ep*), which, when it exists, never presents articulations nor anything that can be called an external or internal skeleton (unless indeed the funnel-cartilages of Cephalopoda be such), and which is generally altogether suppressed in the adult state, its place being supplied by the foot, which, as a development of the central neural region into a locomotive organ, is, so far as I am aware, paralleled throughout the Vertebrata and Articulata by nothing but the dorsal fin of a fish.

In the actual forms, the symmetry of the archetype is almost always disturbed by

in which the shell is wound is the same as that in which the intestine is bent. While the aperture of the shell therefore is "hæmad" in *Atlanta* with regard to the axis of columella, it is "neurad" in *Nautilus* and *Argonauta*.

With an internal shell the reverse appears to be the law. Hence the curvature of the shell of *Spirula* is the opposite of that of the shell of *Nautilus*, and that of a pulmonated Gasteropod is the same as that of a Pectinibranch.

the excessive development of a peculiar region of the hæmal surface, into what has been termed the abdomen or post-abdomen, according as it is placed before or behind the anus.

The integument of this outgrowth, commonly modified in structure and having frequently a prolonged anterior or posterior margin, is the "mantle." It may or may not secrete a shell.

The development of an abdomen (Plate V. figs. 2, 3, 4, 5) produces a corresponding *neural* flexure of the intestine, as in Cephalopoda, Pteropoda and Pulmonata; that of a post-abdomen produces a *hæmal* flexure, as in Heteropoda, Pectinibranchiata, Tectibranchiata and Nudibranchiata (Plate V. figs. 6, 7, 8).

From combinations of these primary changes with subsequent greater or less developments of the various parts of the foot, all the varieties of form in the Cephalous Mollusca are produced*.

The formation of an abdomen with a peculiar development of the margins of the foot into elongated processes, and with cohesion of the posterior epipodial lobes, gives us the Cephalopodan subtype.

The formation of an abdomen with an excessive development of the epipodium, at the expense of the foot-proper, characterizes the Pteropoda.

The formation of an abdomen with a moderate development of the foot-proper, and hardly any of the epipodium, marks the Pulmonate subtype.

The Heteropoda combine a great development of the foot-proper with the formation of a post-abdomen (and only a transitory development of the epipodium?). The Pectinibranchiata seem to differ from them only in degree.

The development of a post-abdomen, coexistent with that of the epipodium, characterizes the Tectibranchiata.

The Nudibranchiata have a post-abdomen and an epipodium in their embryonic condition, but lose both (epipodium?) more or less completely as they attain maturity. The foot-proper is very moderately developed, or even disappears (*Phyllirrhoë*).

If the "mantle" is to have an analogue anywhere among the Articulata or Vertebrata, it may probably be with the carapace of the Crustacea, inasmuch as this is developed from a corresponding region and has similar functions, *i. e.* to protect the respiratory organs.

Hitherto what has been said has referred to the morphology of the external organs. It remains to show on what plan the internal organs are arranged, and how the archetypal arrangement is modified among the different families. To enter upon this subject fully would belong rather to a formal treatise upon the Mollusca. For the present my object is merely to point out the fundamental unity which obtains

* For clearness' sake I have referred to the "hæmal" and "neural" flexures as if they always took place in a vertical plane, whereas, as every one knows, the anal aperture is almost always either to the right or the left in the Gasteropoda. The only modification of the theory required to meet this fact, is to suppose that the hæmal outgrowth takes place more rapidly on one side than on the other.

among certain of the most important systems of organs, and to bring into prominence some facts in the anatomy of the Mollusca which have hitherto been unknown or neglected.

With these views I propose to treat—1, of the nervous system; 2, of the vascular system; 3, of certain portions of the alimentary system; and 4, of the renal system.

1. *Nervous System.*—The nervous system of every Mollusk consists of two great systems;—A. an excito-motor, or sensory and volitional system; B. a visceral or sympathetic system. The former consists of three pairs of primary ganglia, which always exist, and of a variable number of accessory local ganglia, which may or may not exist*.

* The first record I can find of the distinct enunciation of this very important anatomical fact, is in M. Souleyet's essay on the Pteropoda (Observations Anatomiques, Physiologiques et Zoologiques sur les Mollusques Ptéropodes), of which an abstract is given in the Comptes Rendus for 1843: he says,—"The central nervous system of the Mollusca is essentially composed of the three orders of ganglia which I have just pointed out (orders answering exactly to those mentioned in the text), and it is in fact reduced to these ganglia in a certain number of animals of this type. But in others the nerves which are given off present numerous enlargements in their course, and this tendency to a ganglionic disposition is so decided among the highest Mollusks, that all the nerves emanating from the central medullary masses produce new ganglia in the parts to which they are distributed" (p. 667).

Again:—"From the facts which have just been stated summarily, I believe I may conclude,—

"1. That the exclusive analogy which many naturalists have wished to establish between the nervous system of the Mollusca, and one of the portions of the same system in the animals of higher classes, is not only contrary to physiological principles, but also to anatomical facts.

"2. That the nervous system of Mollusks corresponds, in fact, in its distribution to the same parts as those which constitute it in the superior animals, the whole difference consisting in the degree of development and disposition of the parts which is in relation with the rank that Mollusks occupy in the series, and the plan which nature has followed in their zoological type.

"3. That the definition very commonly given of this system in Mollusks, that it is *composed of ganglia scattered in different parts of the body*, is not exact, since the parts which by their fixity ought to be considered as those which essentially constitute it, are always grouped round the œsophagus. The others, in fact, are to be regarded only as different degrees of development of these central portions, which is proved by their degradation or disappearance in proportion as we descend in animals of this series.

"4. That the central nervous system of Mollusca is always double, and consequently symmetrical, in opposition to what some anatomists have advanced; that it hardly differs in this respect from the nervous system of the Articulata, except by the centralization of the locomotive ganglia, a centralization which may be observed in many animals of the latter type.

"5. Lastly, that it has been wrongly asserted as a general rule, that the ganglia of which the nervous circle of the Mollusca is composed, tend to approximate the higher the organization of the animal, the position of these ganglia being essentially subordinate to that of the organs which they have to innervate" (p. 669).

The very just and admirable views here set forth seem to have met with strange neglect; foreigners, however, might be pardoned for this, since M. Souleyet's own countrymen contrive (see Blanchard, Sur l'organization des Opisthobranchies, Annales des Sc. Nat. 1848) five years afterwards not to know anything about them.

See also the memoir of Hancock and Embleton, before cited, in which the first complete demonstration of the true sympathetic system in the Gasteropoda is given; and Alder and Hancock's British Nudibranchiata, in which are contained the most beautiful descriptions and figures of the anatomy of the Mollusca extant.

These three pairs of primary ganglia are the Cephalic, the Pedal, and the Parieto-splanchnic.

I. *The Cephalic Ganglia.*—These are always either in apposition, or are united by a commissure above the œsophagus. They give off either immediately or from the connecting commissure, the following nerves:—

1. Labial, to the lips and anterior parts of the head.
2. Olfactory, to the tentacles.
3. Optic.
4. Buccal, to the buccal mass, tongue, and jaws.

Accessory ganglia may be developed upon all these nerves. They are found upon the labial nerves in *Gasteropteron*, three upon each side (Souleyet and Blanchard); upon the olfactory nerves in many Nudibranchiata (Alder and Hancock, Souleyet, &c.); upon the optic nerves in Cephalopoda and Heteropoda.

The presence of ganglia upon the buccal nerves is almost constant. There seems to be only one inferior buccal ganglion in some Cephalopoda, while in others there are two, one above and one below. In the Heteropoda, Pteropoda, and most Gasteropoda, there is a pair of ganglia placed laterally at the re-entering angle of the œsophagus and buccal mass. In *Patella, Haliotis,* and *Fissurella,* I have found four, two in the latter position, and two anteriorly, just where the buccal nerves come off.

The buccal ganglia are always united by a commissure, so that when the cerebral ganglia are above the œsophagus, an anterior nervous ring is formed; when they are at the side or below, as in Pteropoda, there is no anterior nervous ring.

II. *The Pedal Ganglia.*—These are either in contact or are united by a commissure; *below* the œsophagus they give off—

1. Auditory nerves.
2. Pedal nerves.

The auditory nerves are not commonly present, as their organs are generally sessile; however, they exist in Cephalopoda, and in *Strombus* and *Pteroceras.* As has been stated above, the Heteropoda make an extraordinary exception to the usual position of the auditory organs, since in them these nerves appear to be given off from the cephalic ganglia. Considering, however, that the auditory nerves are invariably attached to the pedal ganglia in all other Mollusks, and that in *Pteroceras* and *Strombus,* genera which so nearly approach the Heteropoda, the auditory nerves are very long, I do not think it very hazardous to suppose, that in the Heteropoda the auditory nerves really proceed from the pedal ganglia, but have become united to the cephalic ganglia.

In any other case their position is quite exceptional, for the supraœsophageal position of the auditory sacs in Nudibranchiatata merely arises from the pedal ganglia being thrust upwards, and united with the cephalic ganglia.

The accessory ganglia of the pedal ganglion appear to be only what may be called

digital ganglia, developed to meet the wants of certain elongations or expansions of the foot.

Such are the ganglia at the bases of the arms of the Cephalopoda, and such appear to me to be the ganglia which supply the "labial" processes of *Nautilus.*

III. Under the name of *Parieto-splanchnic system of ganglia,* I include the branchial and visceral ganglia of most authors, and the cervical, branchio-cardiac, and angeial ganglia of M. BLANCHARD. This system consists of two *primary* ganglia, which are always to be found at the side of the œsophagus, connected with both the pedal and cephalic ganglia, and for which I reserve specially the term *parieto-splanchnic* ganglia; from these nerves are given off—

1. *Parietal,* to the sides of the body, as distinct from the foot.
2. *Columellar,* to the shell-muscle or muscles, of which there are two in *Octopus, Nautilus,* and *Cymbulia*; one in the shelled Gasteropoda.
3. *Branchial,* to the branchiæ.
4. *Angeial,* to the heart and great vessels and generative organs.

Separate ganglia, answering to the three latter sets of nerves, may be found in the dibranchiate Cephalopoda; to the two last in the Heteropoda; a single ganglion corresponding to all of them is found in *Aplysia, Buccinum, Turbo, Paludina,* &c. Two such exist in *Strombus* and *Pteroceras.*

The angeial ganglia, wherever they exist separately, are placed above the aorta and united by a commissure.

The visceral or sympathetic nerves ramify extensively over the intestinal canal (see HANCOCK and EMBLETON upon *Doris*). They are connected anteriorly with the buccal ganglia, posteriorly with the parieto-splanchnic system.

To sum up, the typical number of ganglia in the Cephalous Mollusca is three pair, with which accessory ganglia and visceral ganglia may be connected in variable number. The primary ganglia are united by commissures which form—1, two *greater* nervous rings, the *cephalo-pedal,* connecting the cephalic and the pedal ganglia, and the *cephalo-splanchnic,* connecting the cephalic and parieto-splanchnic ganglia: these rings surround both the œsophagus and the aorta. 2, Two *lesser* nervous rings, the cephalo-buccal, uniting the cephalic and buccal ganglia, and encircling the œsophagus, and the parieto-angeial, uniting the parieto-splanchnic and angeial ganglia, and sometimes surrounding the aorta alone: this ring does not seem to be invariably present.

The homology of these ganglia with those of other animals does not, I think, present any very great difficulty.

It is needless to point out their identity with those of the Acephala Lamellibranchiata.

In the Articulata we have corresponding cerebral ganglia, while the subœsophageal ganglionic chain answers to the pedal and parieto-splanchnic ganglia united. The nerves of the latter system appear in a distinct form as the *transverse* nerves of Insects.

It seems possible that the series of lateral ganglia in certain Annelida (*Amphinome*) may correspond with the parieto-splanchnic ganglia of Mollusks.

On the other hand, the stomato-gastric nerves with their ganglia in Articulata appear to correspond with the visceral nerves of Mollusca.

To what portions of the nervous system of the Vertebrata do these various ganglia answer? This is a problem which has been variously solved. Unless, with Von Baer, we deny the homology of the centres of the nervous system in the Invertebrata with those of the Vertebrata, an argument whose worth can only be decided by a careful and laborious study of development, it would seem clear that the cerebral ganglia are homologous with the corpora striata and thalami of Vertebrata. Their accessories, the buccal ganglia, answer to the trigeminal ganglia, and supply similar parts.

The cephalo-pedal and cephalo-splanchnic commissures correspond with the crura cerebri; the pedal and parieto-splanchnic ganglia answering to the spinal cord and medulla oblongata. The origin of the auditory nerves would then correspond with that of the seventh pair in Vertebrata, and the pedal nerves with the spinal nerves in function and position.

Again, if the parieto-splanchnic ganglia represent the medulla oblongata, their branches should, as I think they do, represent a pneumogastric nerve*.

Finally, the visceral nerves answer to the sympathetic.

The next question to be considered is, in what manner these typical ganglia are arranged and combined to form the almost infinite varieties in the actual nervous systems of the Cephalous Mollusca.

We find—

1. The ganglia concentrated into a mass above the œsophagus, e. g. *Doris*, *Phyllirrhoë*, the majority of the Nudibranchiata.

2. The ganglia concentrated into a mass below the œsophagus, e. g. Pteropoda.

3. The ganglia concentrated around the œsophagus, some above and some below, e. g. *Buccinum*, *Helix*, *Onchidium*, Cephalopoda.

4. The ganglia scattered and separated in pairs, e. g. Heteropoda, Tectibranchiata, and many Pectinibranchiata.

Among these the parieto-splanchnic ganglia may either be united by apposition with the pedal ganglia, and with the cerebral by commissure, as occurs most commonly, e. g. *Octopus*, *Nautilus*, *Haliotis*; or they may be united with the cerebral ganglia by apposition, and with the pedal by commissure, as in *Strombus* and *Pteroceras*.

Patella, *Aplysia* and *Bullæa*, form a gradual transition from one of these conditions to the other.

It will be seen at once from this enumeration that the concentration of the nervous

* Von Siebold compares the nerves which arise between the nerves to the ganglion stellatum in Cephalopoda to a par vagum. Vergl. Anat. p. 379.

system is by no means a test of high organization in the Mollusca, but rather the reverse.

A peculiarity of the Mollusks belonging to the second and third categories, viz. that their infraœsophageal nervous mass is often perforated by the aorta, may be accounted for by the narrowness of the angeial ring, consequent upon the concentration of the elements of the parieto-splanchnic system, so that they unite directly above the aorta.

The singular variation in the arrangement of the different portions of the nervous system, whereby the Mollusca as a class differ so widely from the other great classes of Vertebrata and Articulata, may, I think, find an explanation in the well-known law, that the constancy of a given arrangement of organs greatly depends upon the period at which they appear in embryonic life. If certain organs are formed early, those which come later must obviously accommodate themselves to their predecessors; and any variations which have taken place in the latter will perturb the normal disposition of the former.

Now in the Mollusca, as has been already stated, the neural side of the embryo is the last to be developed, and the nervous system does not make its appearance until the animal has taken its characteristic form.

Contrast this with the Vertebrata; in them the nervous system is the first to be developed, and it is, of consequence, the most fixed and unchanging feature in the whole of their organization.

On the other hand, the separation of the abdomen or post-abdomen from the body is one of the earliest facts in molluscous development, and it has a corresponding influence over their whole organization.

The Archetypal Vascular System and its modifications.—It may be questioned whether the "archetypal" heart has a single or a double auricle, but it is certain that in proportion as the symmetry of the branchial apparatus and of the whole body is preserved, we approach to the form of heart with a double auricle. Thus we have a double auricle in *Chiton* and *Haliotis*, and a close approach to it in *Tethys*, *Janus*, and the *Eolidæ*.

In the Cephalopoda the contraction of the branchio-cardiac veins has been observed by MILNE-EDWARDS and KÖLLIKER, so that they may be considered to be auricles. This is another curious illustration of the fact, that what is commonly considered the most concentrated and highest organization does not occur in the reputed highest forms of Mollusca.

The heart lies above the intestine, and gives off the aorta anteriorly. This runs forwards through the cephalo-pedal ring with the œsophagus, and terminates eventually in the buccal mass. Its main branches may be classed as visceral and pedal.

It is needless to enter here upon the beautiful discoveries of M. MILNE-EDWARDS, with respect to the incompleteness of the circulation in the Mollusca. The facts I

have detailed add ocular proof to his already convincing demonstrations. But it is to be observed, that in this respect, again, the "highest" Cephalopod, *Octopus*, possesses no "higher" organization than the Slug or Snail*

The consideration of the archetypal vascular system leads naturally to that of the value of the distinction made by M. MILNE-EDWARDS between *opisthobranchiate* and *prosobranchiate* Mollusca. If my views be well-founded, it is clear that opisthobranchism is the typical condition of all Mollusks, and that prosobranchism is one result of that asymmetrical development which I have endeavoured to show to be the principal agent in modifying the form of these animals. A little consideration will render it evident, that neither the *neural* nor the *hæmal* flexure will have any effect in altering the position of the heart, so long as the flexure occurs *behind* it, while either flexure will produce prosobranchism, if it take place *before* the heart.

Prosobranchism then indicates that a flexure has taken place, but not in what direction; opisthobranchism indicates only that no flexure has taken place in front of the heart.

As derived characters, therefore, we may expect them to fail in certain cases; and those Mollusks which I have chosen to illustrate this paper are instances of their failure. *Firoloïdes* is nearly opisthobranchiate, while *Atlanta* is very decidedly prosobranchiate; and similar variations, as I have shown, occur among the Pteropoda.

The Archetypal Alimentary Canal consists of—1, lips; 2, jaws; 3, buccal mass and tongue; 4, œsophagus; 5, crop; 6, stomach or gizzard; 7, pyloric appendage; 8, intestine; 9, glandular appendages. I wish here merely to draw attention to some peculiarities of the third and the seventh organs in this list, which have not, I think, been hitherto sufficiently noted.

Of the Structure of the Buccal mass and Tongue (Plate V. figs. 12, 13, 14, 15).—Although the structure of the "tongue" of the Mollusca has been very elaborately investigated, its mechanism appears to me to have been hardly at all understood.

CUVIER, who first described this structure in *Buccinum*, thought that the buccal cartilages were the chief agents in moving the tongue. He considered the 'tongue-plate' to be passive, and that its movements depended upon the protraction, retraction, divergence or approximation of the cartilages†.

This idea is still further carried out in the Leçons d'Anatomie Comparée (2nd ed. t. v. p. 15–25), where the cartilages are compared to rudimentary jaws, though a little consideration would have shown the jaws to be represented by other organs in some of the instances quoted.

Subsequent writers either coincide in CUVIER's view, or substitute for it some vague notion of licking or rasping; so OSLER‡ and TROSCHEL§.

* The "vena cava superior" of Cephalopoda answers to the very short trunk formed by the union of the two afferent branchial trunks in *Aplysia*, &c., which, as receiving the veins of the foot, correspond with the venous circlet at the base of the arms.

† Mém. sur les Mollusques, Grand Buccin, p. 9.

‡ Philosophical Transactions, 1832.

§ WIEG. Arch. 1836.

Middendorf, in his elaborate Monograph upon *Chiton* (Malacozoologia Rossica), gives a very careful and detailed description of the buccal apparatus in that Mollusk, but equally fails in rendering its action clear.

He gives the name of tongue exclusively to a "bifid papillose organ, surrounded by circular folds, which consists mostly of vascular branches, between which masses of muscle are interwoven:" this is placed in the floor of the buccal cavity in front of, and below the buccal mass.

To what is commonly known as the tongue, he gives the name of "radula," "reibplatte." The dentigerous plate is the "lamina radulæ," its expanded portion the "orbis radulæ." What I have called the buccal cartilages are his "folliculi motores."

It is difficult to come at any clear understanding of Middendorf's views, but so far as I can comprehend them, he appears to consider that the "lamina radulæ" acts as a sort of elastic file pushed from behind by a special muscle, the "curvator radulæ," and supported and steadied by the "folliculi motores."

Von Siebold says*, "this organ (the tongue), by its protrusion and retraction, is made use of by the Cephalophora as an ingestive apparatus." He says nothing about the buccal cartilages or the minute structure of the organ.

When I first examined this apparatus carefully six or seven years ago in *Buccinum*, I was convinced that Cuvier had mistaken its mode of operation, and further observation has only strengthened that conviction.

I have already described the manner in which the apparatus may be *seen* working in *Firoloïdes* and *Atlanta*, and I propose now to demonstrate that from the anatomical arrangements the "tongue" has the same chain saw-like mode of operation throughout the Cephalopoda and Gasteropoda. Perhaps *Patella* may be taken as the most convenient illustration, since the organ is here very large, and its parts are distinct and well-developed.

In *Patella* (Plate V. figs, 12, 13) it is an oblong mass, reddish, except where the tongue-plate shines with a somewhat greenish hue. It is bifid posteriorly, and has a sulcus along two-thirds of its upper surface. In this the tongue lies before it enters the cavity of the mouth. The opening of the œsophagus corresponds with about the anterior fourth of the upper surface of the buccal mass.

To the postero-lateral angles of the mass its extrinsic protractor muscles are attached, two on each side. They go to be inserted into the cephalic parietes, two in front of and above, and two behind the supraœsophageal ganglia. The lower ones are united so as to form a broad muscular plate. Two small muscular bands are also sent from the anterior angles of the buccal mass to the skin of the head.

When the muscular expansion formed by the lower protractors is removed, four or five muscular bands (fig. 12 μ) are perceived inserted by their posterior extremities into the posterior and lower part of the "buccal cartilages," and converging anteriorly to be inserted into the lower edge of an "elastic plate."

* Vergleichende Anatomie, p. 320.

From the same point of origin a thick bundle of reddish fibres passes up over the posterior extremity of the cartilages, and is inserted into the upper edge and sides of the "elastic plate." These may be called the intrinsic muscles (fig. 13 μ).

This elastic plate (η) is an elastic transparent membrane, broad posteriorly, and narrower anteriorly, so as to be somewhat heart-shaped. By its superior surface it gives attachment to the "dentigerous plate" (lamina radulæ of MIDD.), on which the teeth are set; inferiorly it is very smooth, and plays over the equally smooth pulley-like surface afforded by the larger *buccal cartilages* (fig. 14). These are four in number, two large and two small accessory ones (δ). The larger are elongated, white, cartilaginous-looking plates, excavated internally, and thick and convex behind; their inner edges are kept together by strong transverse muscular fibres. Their upper edges are in contact, forming the smooth surface mentioned above; the smaller seem to be in a manner sesamoid cartilages; they are connected anteriorly with the tongue-plate and posteriorly with muscular fibres, which are inserted into the larger cartilages.

It is clear that the action of the intrinsic muscular bands (having the insertions described) must be to cause the "elastic plate," and with it the "dentigerous plate," to traverse over the ends of the cartilages, just like a band over its pulley, the cartilages themselves being entirely passive in the matter. The extrinsic bands, again, must serve to protract the whole mass and thrust it more or less firmly against the object to be acted upon.

I have examined *Buccinum*, *Fissurella*, *Doris* *, *Aplysia*, *Bullæa*, *Helix*, *Onchidium*, *Cypræa*, *Pteroceras*, *Sigaretus* and *Vermetus*, and in all I have found a structure essentially similar to that here described; the difference consisting in the greater or less length of the dentigerous plate, and the more or less complete development and isolation of the buccal cartilages. These are the less distinct the more the tongue becomes a mere organ of deglutition. *Aplysia* and *Bullæa*, for instance, have the cartilages united and much softer than in most genera. The structure of the Cephalopod tongue closely resembles that of *Aplysia*; and it has the further peculiarity, that the portion of the floor of the buccal cavity in front of the tongue (true tongue of MIDDENDORF), which is plicated and distinct in most Gasteropods †, is in the Cephalopods raised up into a laminated caruncle (or several) larger than the tongue itself ‡.

This pulley-like structure of the tongue appears to me to be very characteristic of

* See also the description of the "tongue" in this genus by Messrs. HANCOCK and EMBLETON, *loc. cit.* p. 210.

† OSLER, *loc. cit.*, p. 505, describes a soft striated papilla arising from the floor of the mouth in front of the tongue in *Patella*, which, he says, "is probably the organ of taste."

‡ See OWEN, Article 'Cephalopoda,' Cyc. Anat. and Phys. Is the "horny striated substance" supporting the lingual teeth, "which appears to represent the body of an os hyoides" in *Nautilus*, the representative of the buccal cartilages?

the portion of the molluscous type here considered*, and indeed to be peculiar to it. Its occurrence in *Chiton*, therefore, would effectually determine the molluscous nature of that genus, even if there were no other grounds for the conclusion; while the structure of the buccal armature of *Sagitta*, which has been compared to the protruded tongue of a Heteropod, is in fact so totally different as at once to remove it from the Mollusca†.

I may further remark, that the structure of the tongue in the Cephalopoda adds one more link to the very strong chain of affinity between them and the ordinary Mollusca.

Of the Pyloric Sac.—This appears in various forms in a great number of the Mollusca, and seems to be always in special relation with the liver. In *Atlanta*, it has been seen that its glandular parietes form the liver. In the Cephalopoda the hepatic ducts enter its representative, the spiral sac of *Octopoda*, the elongated sac of *Loligo*. The extreme length of the pyloric sac in *Cleodora*, and the occurrence of a second smaller one, appear to be leading the way to the ramified prolongations of the intestinal canal found in the *Eolidæ*.

In *Pteroceras* a very remarkable structure exists, which, so far as I am aware, has not yet been noticed‡. The existence of a "crystalline style" in connexion with the alimentary canal, has long been known in the Lamellibranchiata, but it has hitherto been supposed to be confined to them. However, in *Pteroceras*, the pyloric sac contains a very complete style, Plate V. figs. 16, 17.

The stomach is a wide somewhat quadrangular cavity. The œsophagus opens into

* It has been noticed by TROSCHEL (Anatomie von *Ampullaria Urceus*, WIEG. Arch. 1845), that the structure of the tongue is the same throughout those Mollusks which have a head: "Under the jaw lies the anterior part of the so-called tongue, a membrane which is present in all Pteropoda, Cephalopoda, Gasteropoda, in short, in all those Mollusks which possess a head. It is wanting in all the so-called Acephala, in the Bivalves and in the Tunicata. It rests, as in all cases where it is present, upon two portions of cartilage of whitish colour, combined by a membrane and moved by many muscles." It is clear, however, from this passage, that TROSCHEL has not recognized the true mechanism of the organ.

† There is a curious similarity between the "tongue" of the Mollusca and the arrangement of the dental apparatus in the Plagiostome fishes, which may be viewed perhaps as another illustration of Von BAER's law, that while the exterior of a vertebrate animal is Articulate in its construction, the interior is Molluscous.

‡ Since writing the above, I find that so far back as 1829, the existence of this organ was distinctly pointed out, though strangely enough the fact has been quite overlooked by every one save VON SIEBOLD; he, however, merely refers to the statement in a note, and says he "does not know what to make of it." (Vergleichende Anatomie, p. 312.) This statement is contained in a valuable paper upon the anatomy of the Mollusca, entitled "General Observations on Univalves," by Mr. CHARLES COLLIER, Staff-Surgeon at Ceylon; printed in the Edinburgh New Philosophical Journal for 1829, p. 231. "There is an organ, the crystalline stiletto, confined erroneously by a celebrated naturalist (CUVIER) to bivalves, which is found in every species of *Strombus*, in *Trochus turritus*, and a species (*Vertagus*) of *Murex*. It is enclosed in a sheath, that passes parallel to and by the side of the œsophagus, to the stomach, into which the stiletto enters, leaving its covering; that end which lies within the stomach is obtuse, laminated, and fixed by a hook of similar substance to its situation. The upper portion is circular, homogeneous, slightly tapering, transparent, of gelatinous consistence, and resembling somewhat a pistil with its stigma."

its left anterior angle, while its pyloric orifice, very close to this, is at the right anterior angle. Behind the pyloric orifice the rounded head of the crystalline style projects from the aperture of the pyloric sac, γ, fig. 16.

Two wide apertures communicate with the liver, and act as hepatic ducts.

Several considerable ridges of the gastric membrane rise from the floor of the stomach; the principal one is next to the cardia, and there is a smaller between the cardia and pylorus. The aperture of the pyloric sac is surrounded by an elevated circular ridge, which is slit towards the pylorus, the left edge of the slit overlapping the right. The end of the style projecting from this orifice is opposed by one or two cartilaginous plates upon the principal elevation. It is only the end of the style which is free; for the rest of its length (2 or 3 inches) it lies in the pyloric sac (λ, fig. 17), which runs back over the intestine, in the thickness of the left side of the mantle, and terminates by a rounded extremity.

It seems probable that the "crystalline style" is secreted by the pyloric sac, and that it acts as a gastric plate, assisting in the comminution of the food, although its transparent and delicate texture would not seem to fit it for the performance of any very important office of this kind.

Its resemblance in position and structure to the crystalline style of *Solen* is sufficiently remarkable.

Renal System.—It has been shown that in the Heteropoda and Pteropoda a "contractile sac" exists, placed so as to be bathed by the blood entering the auricle. It has been hinted that this is a renal organ, and I now proceed to give the reasons for my belief that it is so.

A hollow sacculated organ, with yellowish glandular parietes, surrounds the base of the pulmonary sac in the Pulmonata, and opens by the side of the rectum. The secretion of this organ has been shown to contain uric acid*. No contractions have been observed in it.

In *Fusus*, *Cypræa* and other Pectinibranchiata, an aperture, frequently seated upon a kind of papilla placed at the posterior and upper part of the branchial chamber, leads into a wide cavity, which is in relation above with the pericardium, and on the sides with the rectum and generative duct. In its anterior wall a yellow gland is frequently attached, which consists of large vascular laminæ. I observed no contractions of either the sac or the yellow gland, but my attention was not at the time particularly directed to this point.

Now I think that this sac, with its vascular gland, is exactly comparable in position to the "contractile sac" and to the renal organ of *Pulmonata*, while, on the other hand, it closely resembles the serous chambers with their contained venous appendages, which open into the mantle-chamber of the Cephalopoda.

The venous appendages of the Cephalopoda, however, have been demonstrated to be renal organs by containing secreted uric acid, and they possess the faculty of rhythmical contraction†.

* H. MECKEL, MÜLLER's Archiv, 1846.

† KÖLLIKER, Entwickelungsgeschichte d. Cephalopoden.

The chambers of the venous appendages, then, in the Cephalopoda answer to a "contractile sac," in which the secreting power and the contractile faculty have become restricted and localized in a portion of the organ*.

I have here touched mainly upon the less commonly understood portions of the internal anatomy of the Cephalopoda and Gasteropoda, but they clearly tend to strengthen the conclusion to be derived from embryology and the more generally known anatomical facts, viz. that the Cephalopoda and Gasteropoda are morphologically one, are modifications of the same archetypal molluscous form.

On the other hand, I have made no reference to the Acephala, nor is it my intention to go into that part of the subject; but, for the sake of the zoological bearings of the question, I may shortly express my belief, that of the two families of the Acephala, there is abundant evidence, both anatomical and embryological, to show that the one, the Lamellibranchiata†, is modelled upon the archetype of the Cephalous Mollusca.

Such evidence as we possess with regard to the Brachiopoda, however, is purely anatomical, and (though I am aware that a great weight of authority lies upon the other side) yet Mr. HANCOCK's opinion, that they are rather to be considered as allied to the Polyzoa than to the Cephalous Mollusca, seems to be quite as plausible as the more general notion.

Should this highly ingenious suggestion be found by embryology to be correct, the Brachiopoda will have the same relation to the Polyzoa as the simple Ascidians to the compound Ascidians, and will form a parallel group to the former in M. MILNE-EDWARDS's section of "*Molluscoïdes.*"

In conclusion, I would observe, that the archetypal Cephalous Mollusk (as thus defined) is, in all its modifications, sharply separated from other archetypes, whatever apparent resemblances or transitions may exist. In all cases these will, I believe, on close examination, be found to be mere cases of analogy, not of affinity.

As CUVIER long ago remarked of the Cephalopoda and Fishes, so we may say of the Cephalous Mollusca in general and other types:—"Whatever BONNET and his followers may say, Nature here leaves a manifest hiatus among her productions." For instance, great as are the apparent resemblances between a Lamellibranch and an Ascidian, they all vanish upon closer examination‡. Neither in its anatomical nor in its embryo-

* A renal organ of similar character has been long since demonstrated in the Lamellibranchiata. (See VON SIEBOLD, Vergl. Anat.)

† The Lamellibranchiata are as truly cephalous as many Pteropoda, and the possession of a distinct head is so much a question of degree as to be a very unfit classificatory character.

‡ I beg that I may not be misunderstood here. While I consider that there is no transition between the Cephalous Mollusca as such, and the Ascidians or Polyzoa, I also fully believe (and so far as the Ascidians are concerned I have endeavoured to demonstrate, Report on the Structure of the Ascidians, already referred to) that the archetype of the Cephalous Mollusca, that of the Ascidians and that of the Polyzoa, are all referable to a common archetype, the archetype of the Mollusca generally. It is one thing to believe that certain natural

logical relations does the branchial sac of an Ascidian correspond with the mantle-cavity of a Lamellibranch.

The nervous system is totally different. The three pairs of ganglia, which exist in all Lamellibranchiata (even the apodal genera), are replaced by one in the Ascidians, which is not homologous (as is commonly asserted) with the branchial ganglion, or intersiphonic ganglion of Lamellibranchiata, but with their pedal ganglion.

The organization of the circulatory system is wholly different. The Ascidians have a cellulose test, not a calcareous shell. The larval conditions are totally distinct.

If, however, all Cephalous Mollusks, *i. e.* all Cephalopoda, Gasteropoda and Lamellibranchiata, be only modifications by excess or defect of the parts of a definite archetype, then, I think, it follows as a necessary consequence, that no anamorphism takes place in this group. There is no progression from a lower to a higher type, but merely a more or less complete evolution of one type.

It may indeed be a matter of very grave consideration whether true anamorphosis ever occurs in the whole animal kingdom. If it do, then the doctrine that every natural group is organized after a definite archetype, a doctrine which seems to me as important for zoology as the theory of definite proportions for chemistry, must be given up.

Description of the Plates.

In all the Plates the same letters refer to the same parts.

a. Anus.
b. Buccal mass.
c. Contractile sac.
d. Subspiral ciliated band.
ep. Epipodium.
f. Salivary gland.
g. Tentacles.
h. Head.
i. Eye or optic nerve.
j. Auditory vesicle or nerve.
k. Stomach.
k'. Pyloric cæcum.
l. Liver.
m. Mantle.
mt. Metapodium.
ms. Mesopodium.
n. Branchiæ.
o. Ovary.
p. Penis.
pp. Propodium.
q. Abdomen.
r. Post-abdomen.
s. Vesicula seminalis.
t. Testis.
u. Auricle.
u'. Venous canal.
v. Ventricle.
w. Aorta.
w'. Recurrent artery.
x. Cerebral ganglia.
y. Pedal ganglia.
y'. Pedal artery.
z. Parieto-splanchnic ganglia.

groups have one definite archetype or primitive form upon which they are all modelled; another, to imagine that there exist any transitional forms between them.

Every one knows that Birds and Fishes are modifications of the one vertebrate archetype; no one believes that there are any transitional forms between Birds and Fishes.

β. Buccal ganglia or nerves.
γ. Crystalline style.
λ. Its sheath.
δ. Accessory cartilages of the buccal mass.
θ. Tongue plate.
η. Elastic plate.
μ. Muscles.

PLATE II.

Fig. 1. *Firoloïdes Desmarestii.* (Magnified.) Male.
Fig. 2. *Firoloïdes Desmarestii.* Female. Posterior extremity from the left side.
Fig. 3. *Firoloïdes Desmarestii.* Female. Posterior extremity from the right side.
Fig. 4. Penis of the male.
Fig. 5. Egg-tube.
Fig. 6. Nervous system, with the termination of the pedal artery at y'.
Fig. 7. Cerebral ganglia from below.
Fig. 8. Right eye and tentacle.

PLATE III. *Atlanta Lesuerii.*

Fig. 1. Animal in its shell (much magnified), from the right side. Male.
Fig. 2. The same from the left side, to show the arrangement of the nervous and vascular systems.
Fig. 3. Post-abdomen, without the shell; more enlarged, from the right side.
Fig. 4. Portion of the mantle-cavity and post-abdomen from the left side, to show the arrangement of the heart and branchiæ.
Fig. 5. Portion of the penis.
Fig. 6. Cerebral ganglia, from the left side.

PLATE IV.

Fig. 1. *Pneumodermon* ——? A young specimen, to show the form of the foot and its relations.
Fig. 2. *Euribia Gaudichaudii* (Eydoux and Souleyet), from behind, placed, not as it swims, but so as to leave its parts in their normal position. This has been done with each of the figures in this Plate, except it be otherwise expressly mentioned.
Fig. 3. The head and foot of *Euribia,* seen from below.
Fig. 4. *Cleodora curvata* (Eydoux and Souleyet), from the neural side.
Fig. 5. The same, from the hæmal side.
Fig. 6. *Cleodora aciculata,* from the right side, without the shell.
Fig. 7. The same. The head and alæ from the neural side.

PLATE V.

The first eleven figures are to be regarded as mere diagrams, illustrative of the archetypal form of the Mollusca and its more important modifications.

The shaded portion is the hæmal surface, the unshaded the neural surface.

Figs. 2 and 3 are supposed to represent the development of an abdomen, and the changes of position thence undergone by the intestine and heart.

Fig. 4 is a diagram of a Pteropod, corresponding with fig. 2.

Fig. 5 is a diagram of a Cephalopod, corresponding with fig. 3; but in these, changes in the different parts of the foot have been also effected.

Figs. 6 and 7, similarly are supposed to represent the development of a post-abdomen.

Fig. 8. A diagram of *Aplysia*, corresponding with fig. 6. *Atlanta* corresponds exactly with fig. 7.

Figs. 9, 10, 11, are imaginary sections of a Mollusk, a Fish and an articulate animal, respectively, to show the relations of the nervous, alimentary, vascular and appendicular systems.

The Mollusk and articulate animal are in their normal position; the fish is turned upon its back to correspond with them. * The pectoral fins. † The legs of the articulate animal.

Figs. 12–15. The buccal apparatus or tongue of *Patella*.

Fig. 12. From the right side.

Fig. 13. From above.

Fig. 14. The supporting cartilages.

Fig. 15. The elastic plate which plays over them.

Figs. 16, 17. The stomach of *Pteroceras*.

Fig. 1.

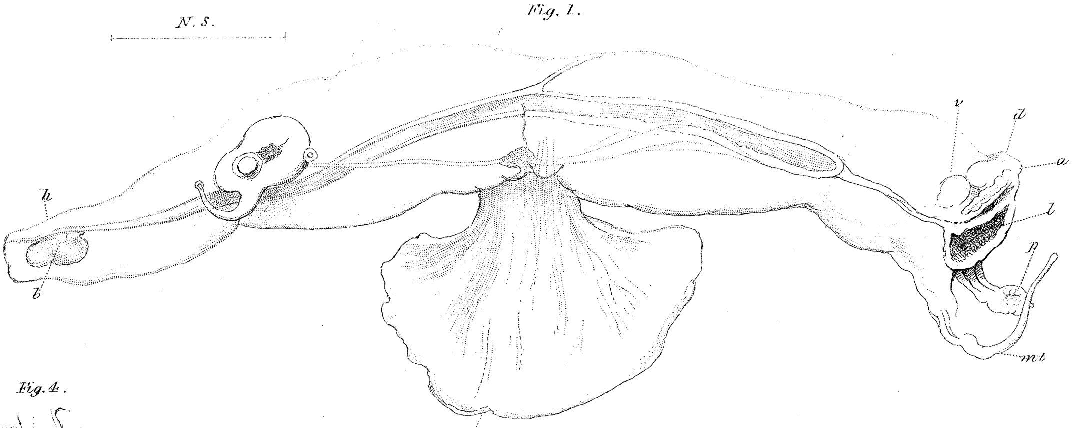


Fig. 4.

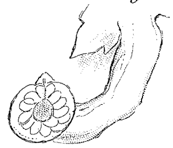


Fig. 2.

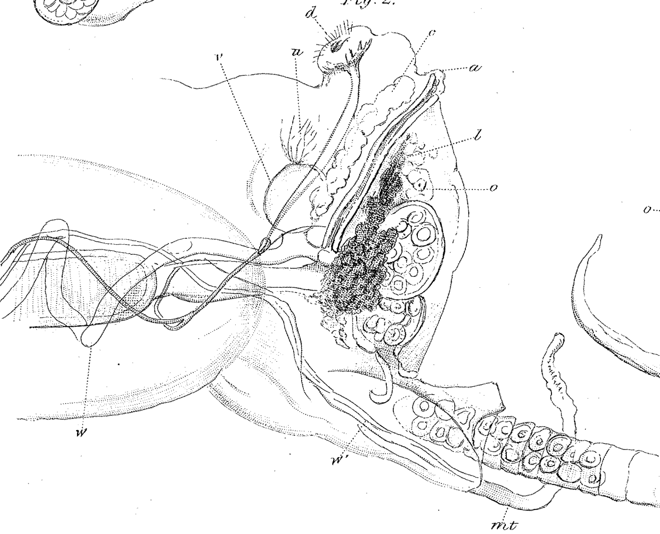
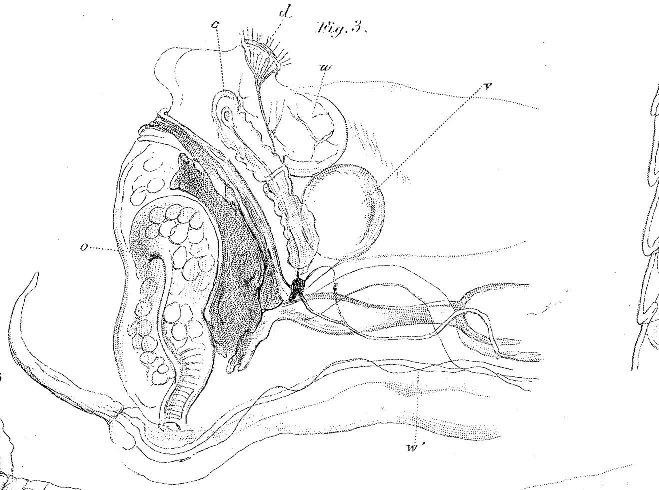


Fig. 3.



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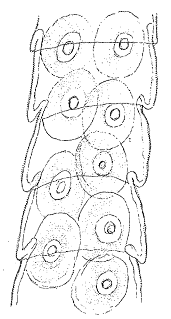

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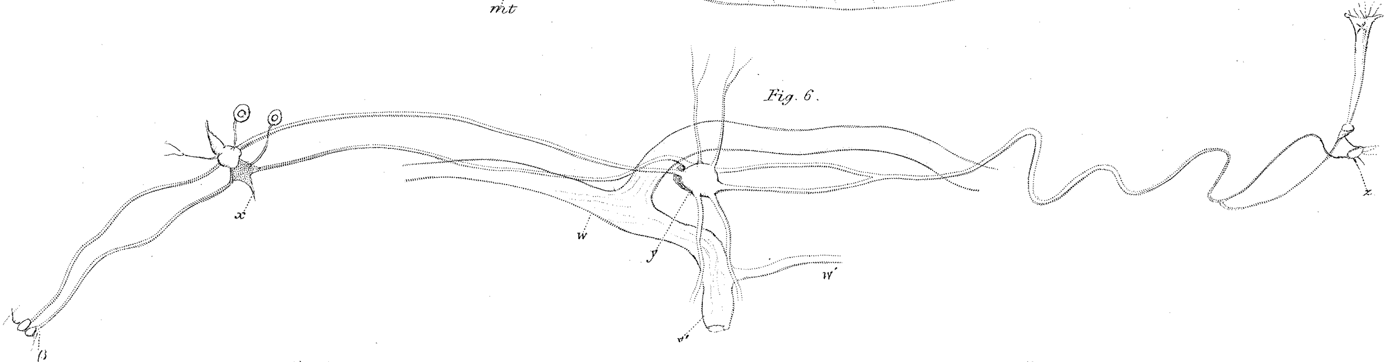

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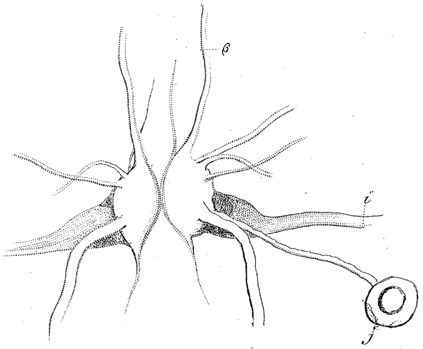

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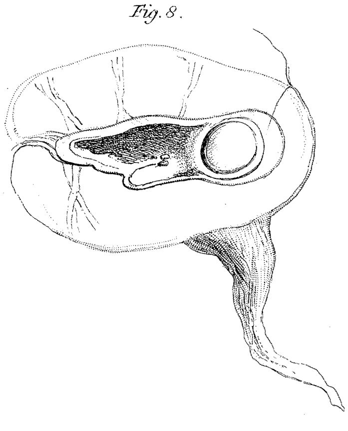

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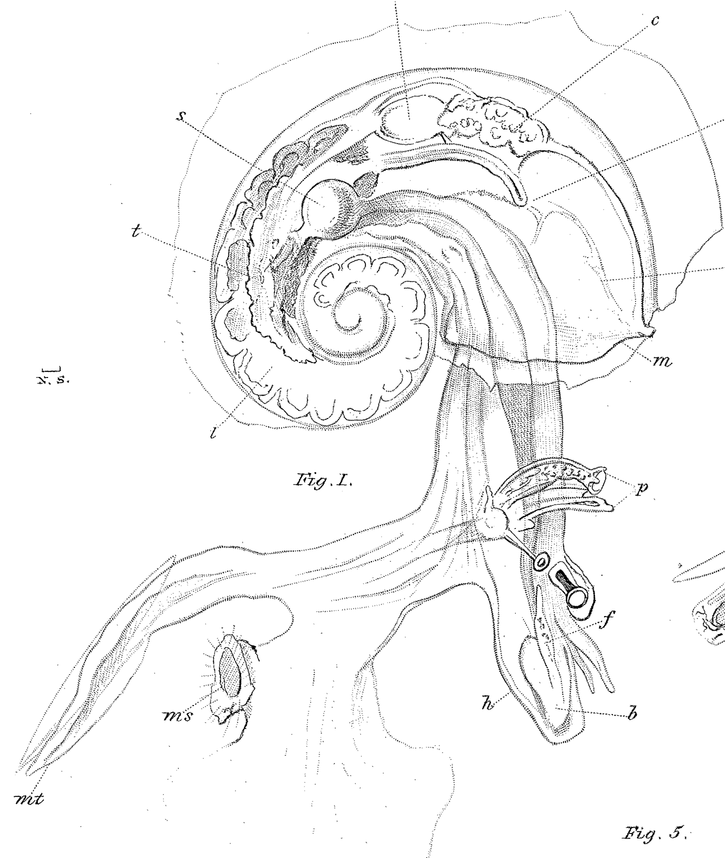
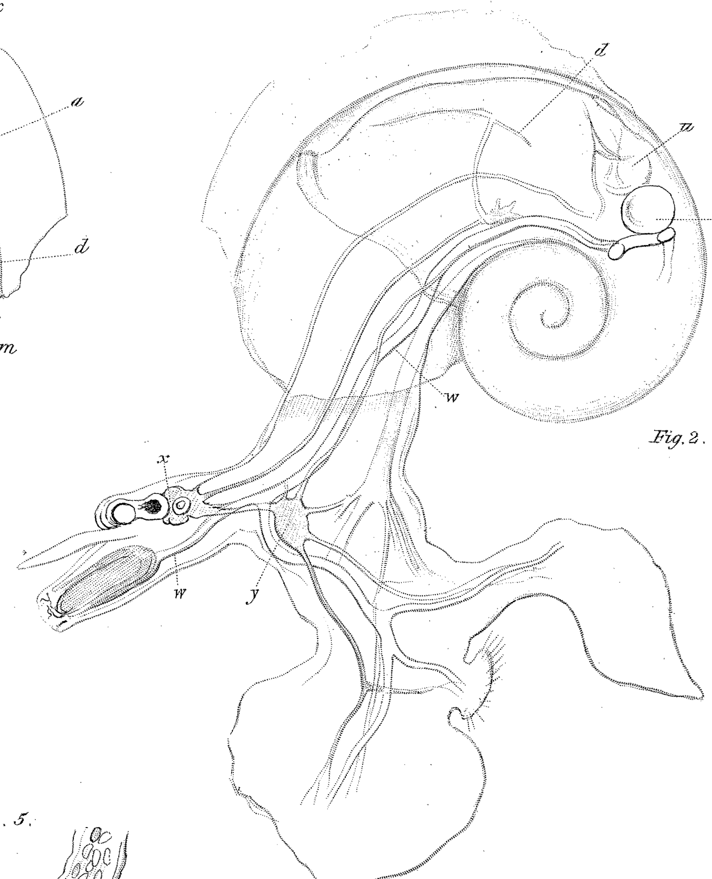


Fig. 1.



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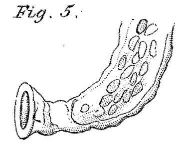


Fig. 5.

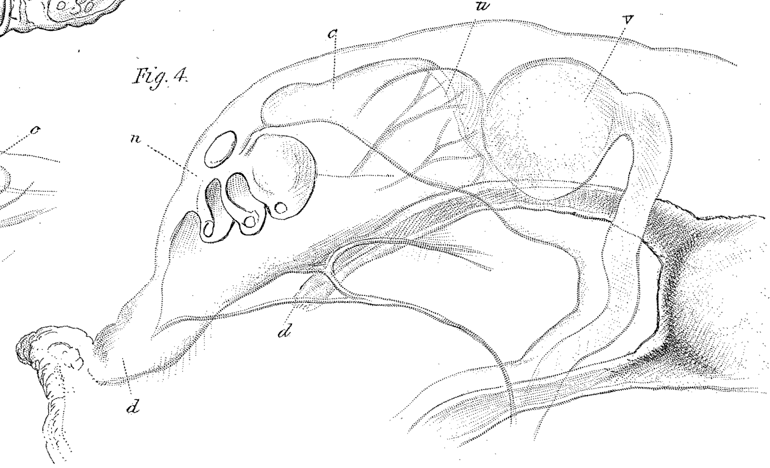
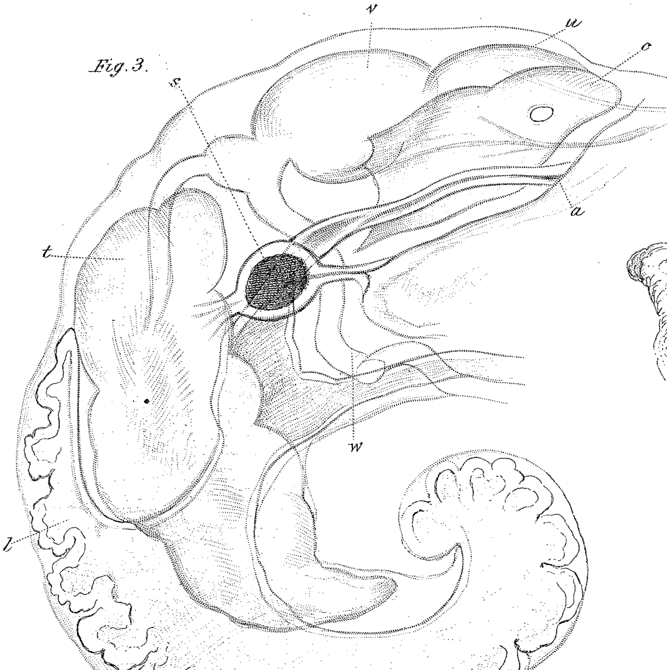


Fig. 4.



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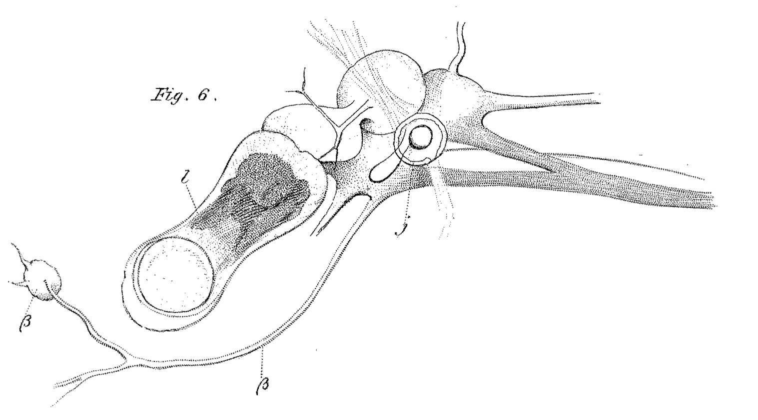


Fig. 6.

Fig. 1.

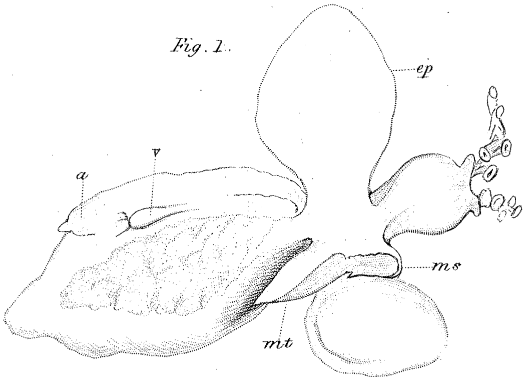


Fig. 2.

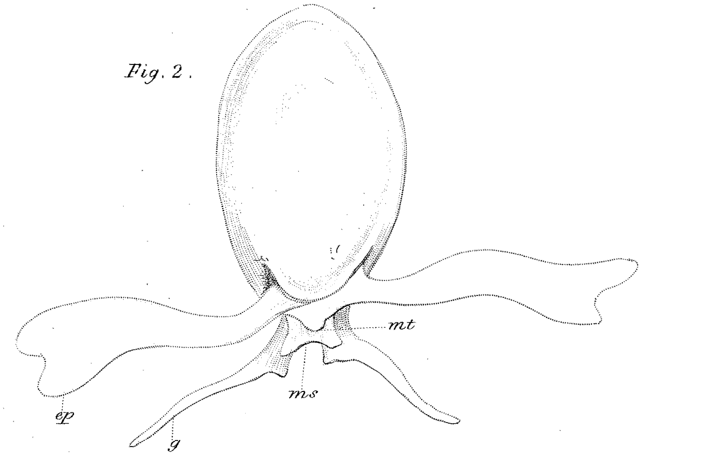
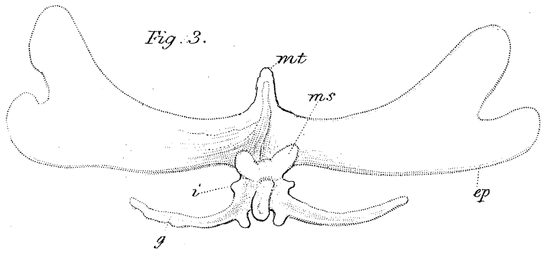


Fig. 3.



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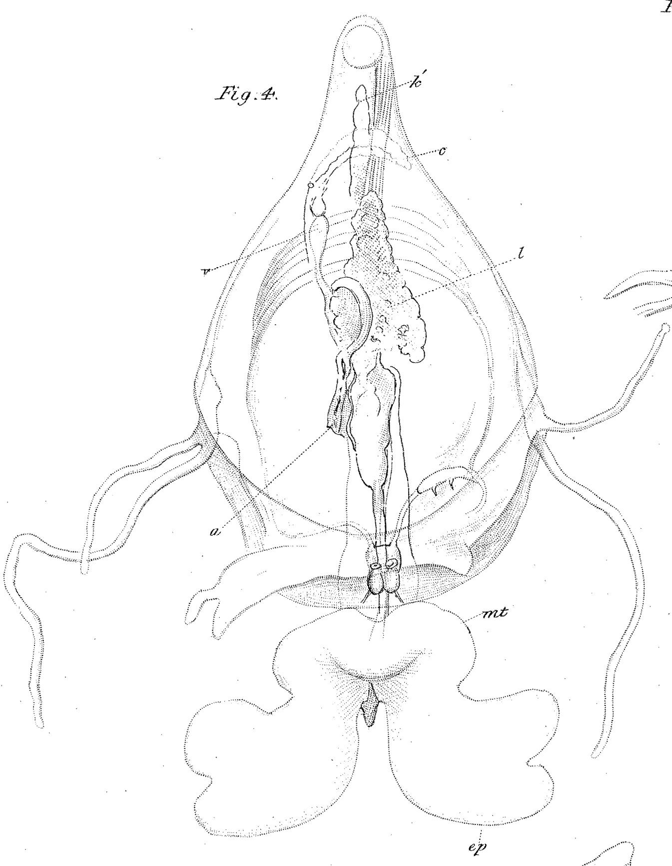
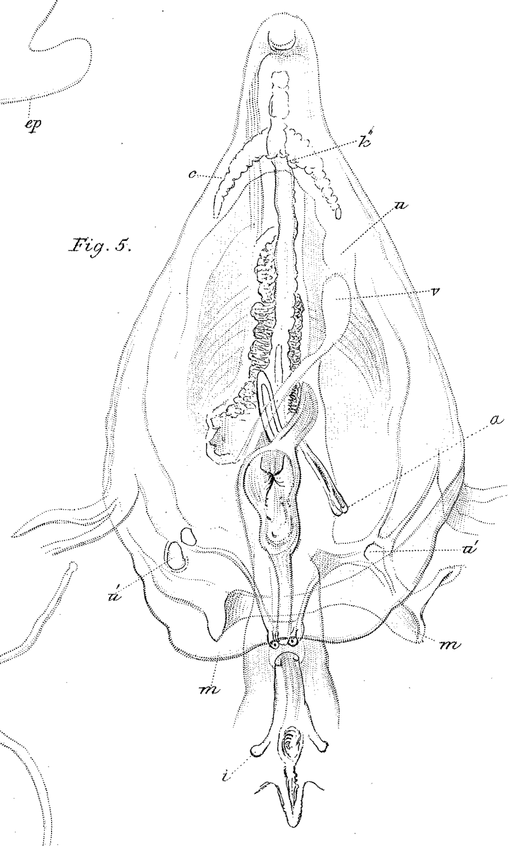


Fig. 5.



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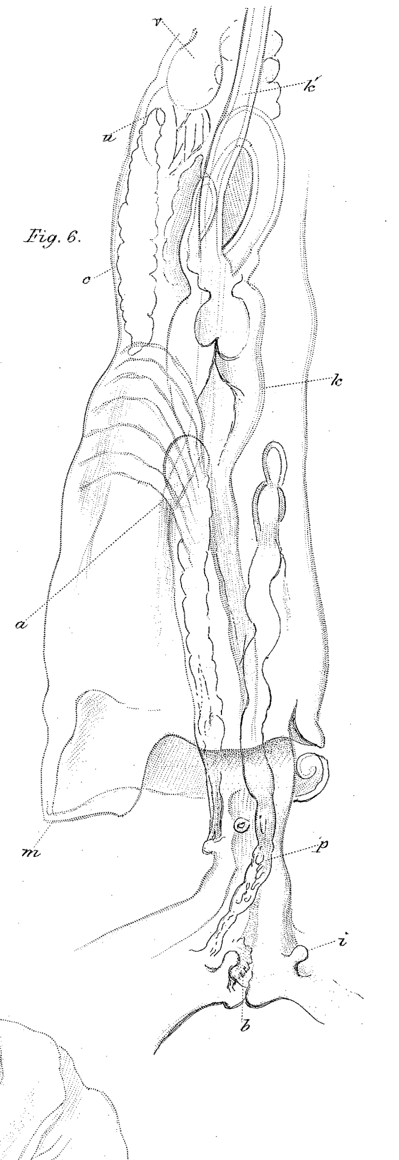
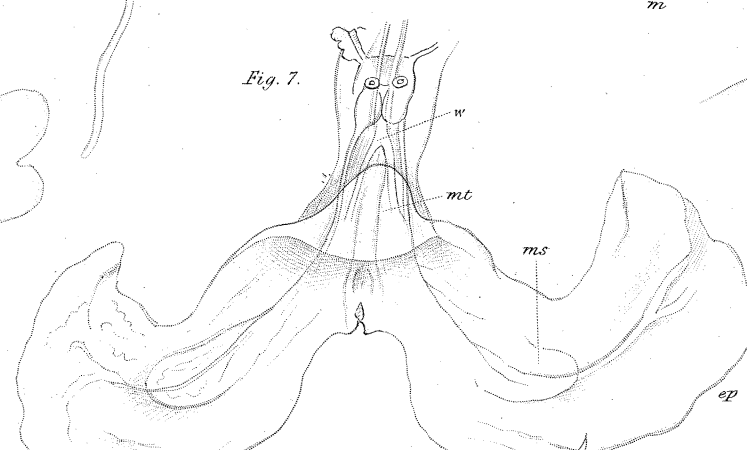


Fig. 7.



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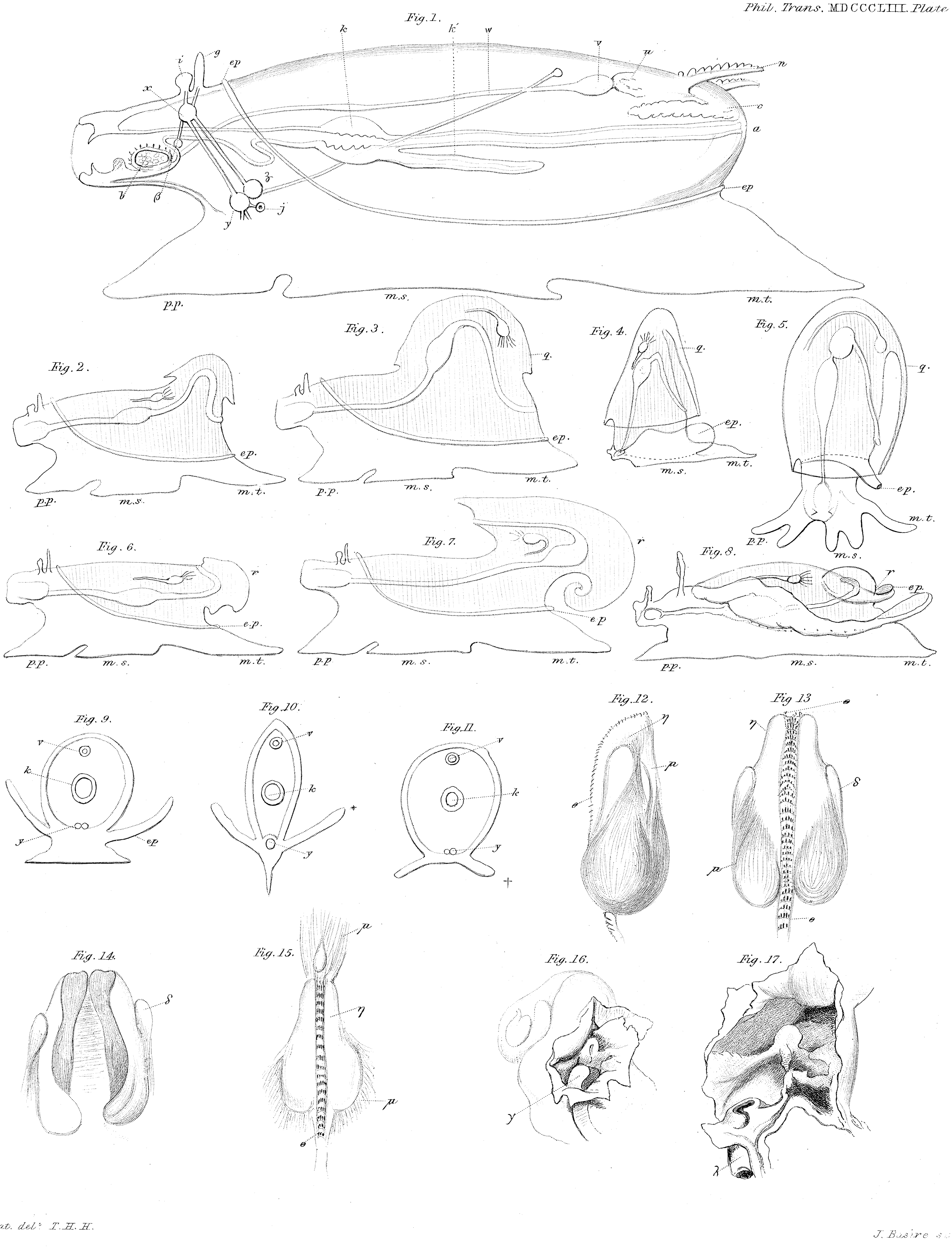

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